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# Cephalic Sensory Canals, Pitlines, and the Classification of Esocoid Fishes, with Notes on Galaxiids and Other Teleosts

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## ABSTRACT

In both the Esocidae and Umbridae, phyletic trends involve reduction of cephalic sensory canals and elaboration of pitlines. Advanced characters of this sensory system indicate interrelationships among Recent species, most notably a close relationship between *Dallia* and *Umbra*. The Eocene *Palaeoesox* and the Oligocene *Proumbra* are attributable to the Umbridae and are probably closely related to *Umbra*. The historical biogeography of the Umbridae may involve a secondary distribution (*Umbra limi*, *U. pygmaea*) in east North America. A relationship between esocoids and galaxiids is unsupported, but a relationship between clupeomorphs and elopomorphs is supported by the structure of the cephalic canal system.

## INTRODUCTION

The cephalic sensory canals and pitlines of esocoid fishes share certain peculiarities with those of galaxiid fishes (including retropinnids and aplochitonids). Some or all of the peculiarities, which involve sensory-canal reduction and pitline elaboration, appear to have developed independently in both groups. The overall trends of both groups may involve some parallelism and consequently a secondary degree of phyletic relation-

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ship. The patterns within each group are, however, of some relevance for assessing intragroup relationships.

## Material and Methods

The present study is based on adult specimens and some serially sectioned juveniles. Specimens selected for illustration were photographed while submerged in 40 per cent isopropyl alcohol. Drawings of pores and pitlines were made by tracing from the photographs. Canals on the specimens were subsequently dissected and added freehand in diagrammatic form to the drawings. Where a canal lies deep to and is crossed by a pitline the canal is shown as interrupted. For illustrated specimens, head length is given in millimeters.

## Institutional Abbreviations

AMNH, the American Museum of Natural History
ANSP, Academy of Natural Sciences of Philadelphia
MCZ, Museum of Comparative Zoology, Harvard University
MLU, Geiseltalmuseum, Martin-Luther-Universität, Halle-Wittenberg
ROM, Royal Ontario Museum
UMMZ, Museum of Zoology, University of Michigan

## Anatomical Abbreviations

AC, antorbital canal
AL, antorbital pitline
ANL, anterior pitline
CL, cheek line
EC, extrascapular canal
EHC, ethmoidal canal
EHL, ethmoidal pitline
EL, extrascapular pitline
IC, infraorbital canal
ICA, anterior infraorbital canal
ICM, middle infraorbital canal
ICP, posterior infraorbital canal
IL, infraorbital pitline
ILA, anterior infraorbital pitline
ILP, posterior infraorbital pitline
MC, mandibular canal
ML, middle pitline
MLI, mandibular pitline
MML, mentomandibular pitline

MPPL, mandibulopreopercular pitline
OL, opercular pitline
POL, postocular pitlines
PPC, preopercular canal
PTC, posttemporal canal
SC, supraorbital canal
SL, supraorbital pitline
SNL, subnasal pitline
TC, temporal canal

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## RESULTS AND DISCUSSION

The cephalic canal system of esocoid fishes (figs. 1–12) includes the following paired components: (1) a mandibular canal (MC, with about 2–9 pores); (2) a preopercular canal (PPC, 4–6 pores); (3) an infraorbital canal (IC, 2–10 pores), which is discontinuous in some species, forming separate anterior (ICA), middle (ICM), and posterior (ICP) parts; (4) a supraorbital canal (SC, 4–6 pores); (5) a temporal canal (TC, 2–3 pores); (6) an extrascapular canal (EC, 3 pores); (7) a posttemporal canal (PTC, 2 pores).

The cephalic pitline system of esocoid fishes includes the following paired components: (1) a mentomandibular line (MML); (2) a mandibular line (MLI; a definitive mandibular line is here considered present only when a mandibular canal is absent); (3) a mandibulopreopercular line (MPPL); (4) an opercular line (OL); (5) a cheek line (CL); (6) an ethmoidal line (EHL); (7) a subnasal line (SNL); (8) an antorbital line (AL); (9) an infraorbital line (IL), which may have discontinuous anterior (ILA) and posterior (ILP) parts; (10) an anterior line (ANL); (11) a

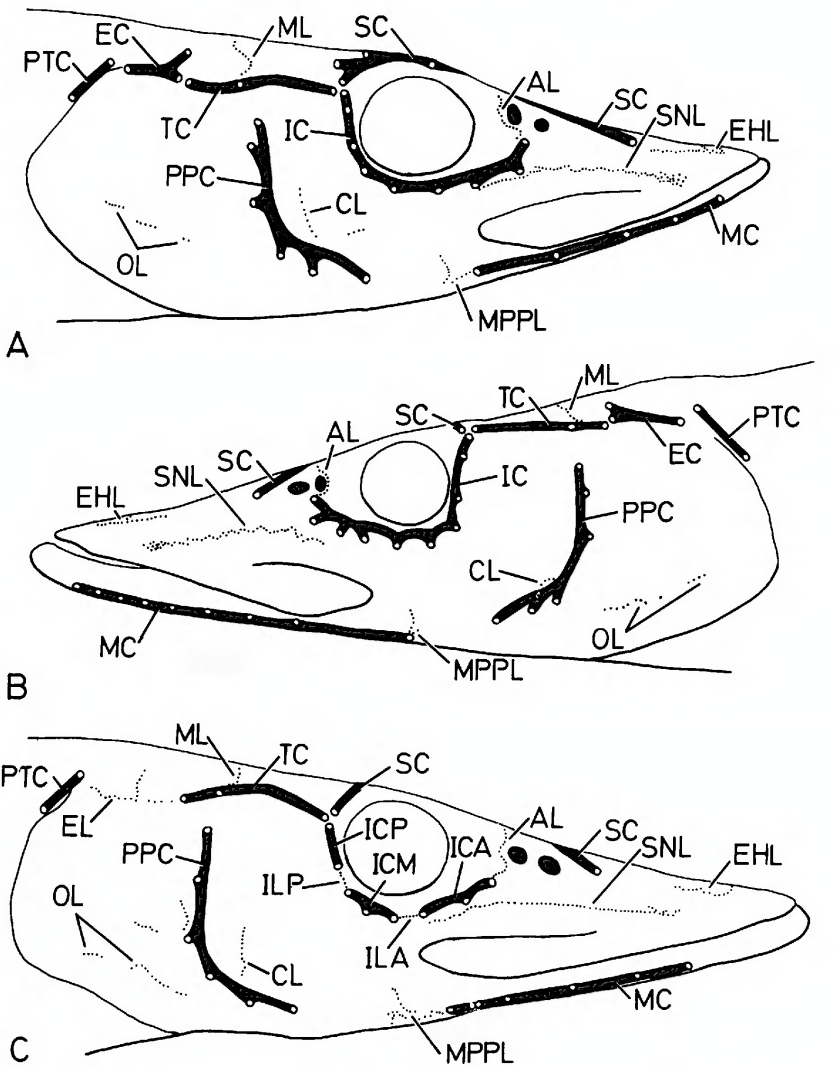


FIG. 1. Cephalic sensory canals, pores, and pitlines, lateral view. A. *Esox lucius*, AMNH 20268, 40 mm. B. *Esox masquinongy*, AMNH uncatalogued, 88 mm. C. *Esox americanus "vermiculatus,"* AMNH uncatalogued, 56 mm.

middle line (ML); (12) an extrascapular line (EL) (see also Tretjakoff, 1941; Schwartz and Hasler, 1966).

Comparisons may be made between esocoids and teleosts such as *Elops*, *Megalops*, *Hiodon*, *Salanx*, *Thymallus*, *Hoplias*, and *Osmerus* (figs. 13–16). In them the canals are generally interconnected (with the exceptions of the supraorbital canal of *Hiodon* and *Hoplias*, and the mandibular canal of *Salanx*). Pores are relatively numerous and pitlines few. On this basis,

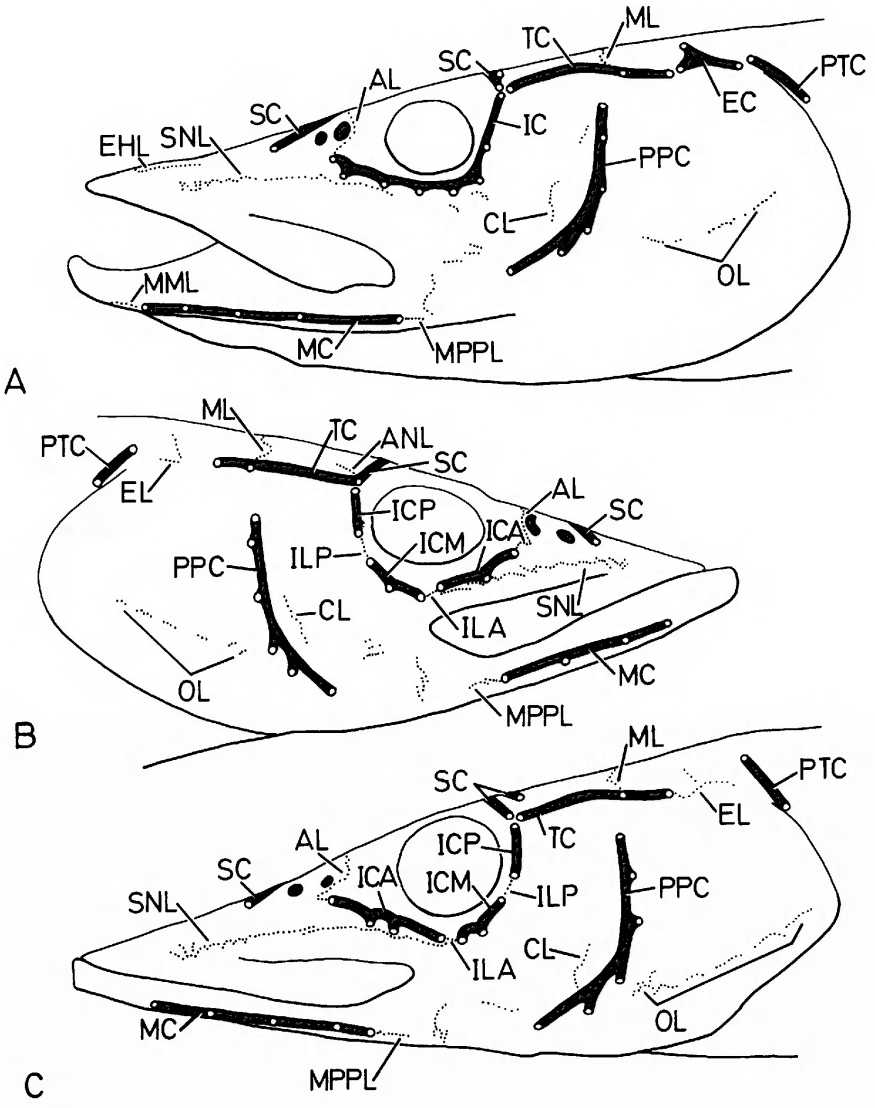


FIG. 2. Cephalic sensory canals, pores, and pitlines, lateral view. A. *Esox reicherti*, ROM 25878, 126 mm. B. *Esox americanus "americanus,"* AMNH 27716, 34 mm. C. *Esox niger*, AMNH 23714, 47 mm.

and what is known about the sensory canal system of other vertebrates (e.g., Allis, 1934, 1935; Holmgren, 1942; Stensiö, 1947; Holmgren and Pehrson, 1949), one may hypothesize that the canal pattern primitive for teleosts comprised an interconnected series of mandibular, preopercular, ethmoidal, antorbital, infraorbital, temporal, extrascapular, and post-

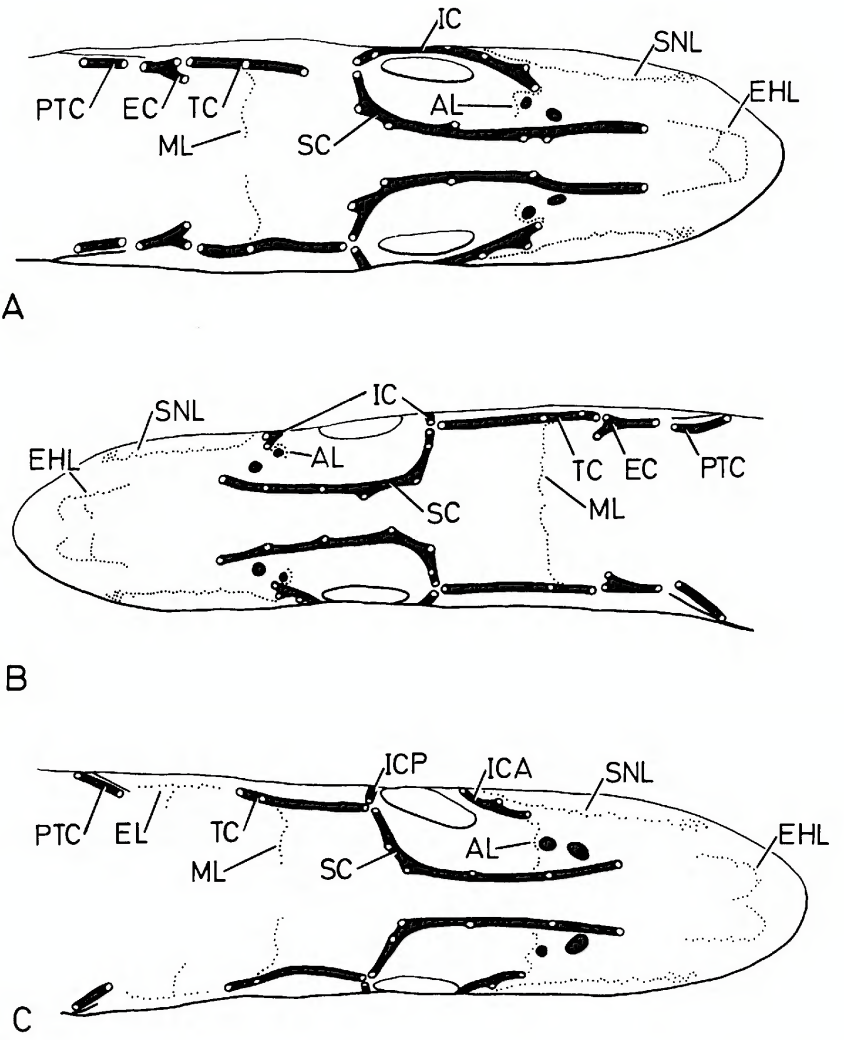


FIG. 3. Cephalic sensory canals, pores, and pitlines, dorsal view. A. *Esox lucius*. B. *Esox masquinongy*. C. *Esox americanus*"*vermiculatus*."

temporal canal components; the supraorbital canal, however, may have been independent, as it is in *Hiodon* and *Hoplias*. Similarly one may hypothesize that the pitline pattern primitive for teleosts comprised a mento-mandibular line, a cheek line, an anterior line, and a middle line.

Comparisons may be made between this primitive pattern and the patterns of esocoids. On this basis, one may hypothesize that the canal and pitline pattern primitive for esocoids was approximately that shown by the species *Esox lucius*, *E. reicherti*, and *E. masquinongy*. If so, characters

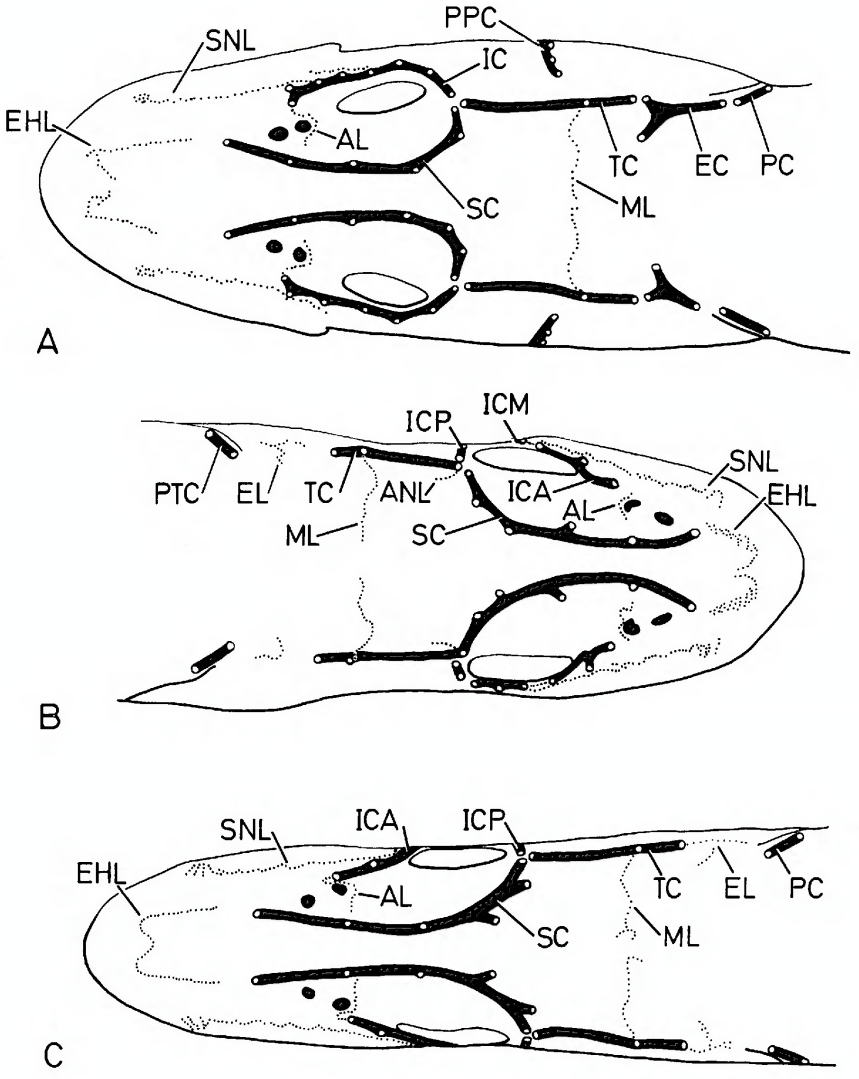


FIG. 4. Cephalic sensory canals, pores, and pitlines, dorsal view. A. *Esox reicherti*. B. *Esox americanus* "*americanus*." C. *Esox niger*.

that developed during the differentiation of the esocoid pattern from that primitive for teleosts include (1) reduction of canals from a continuous to a discontinuous system; (2) elaboration of certain pitlines.

All esocoids have the canal components partly or wholly independent of one another (the temporal, supraorbital, and infraorbital canals open near one another, behind the eye, and some degree of confluence may occur in that position). All esocoids have mandibulopreopercular, sub-

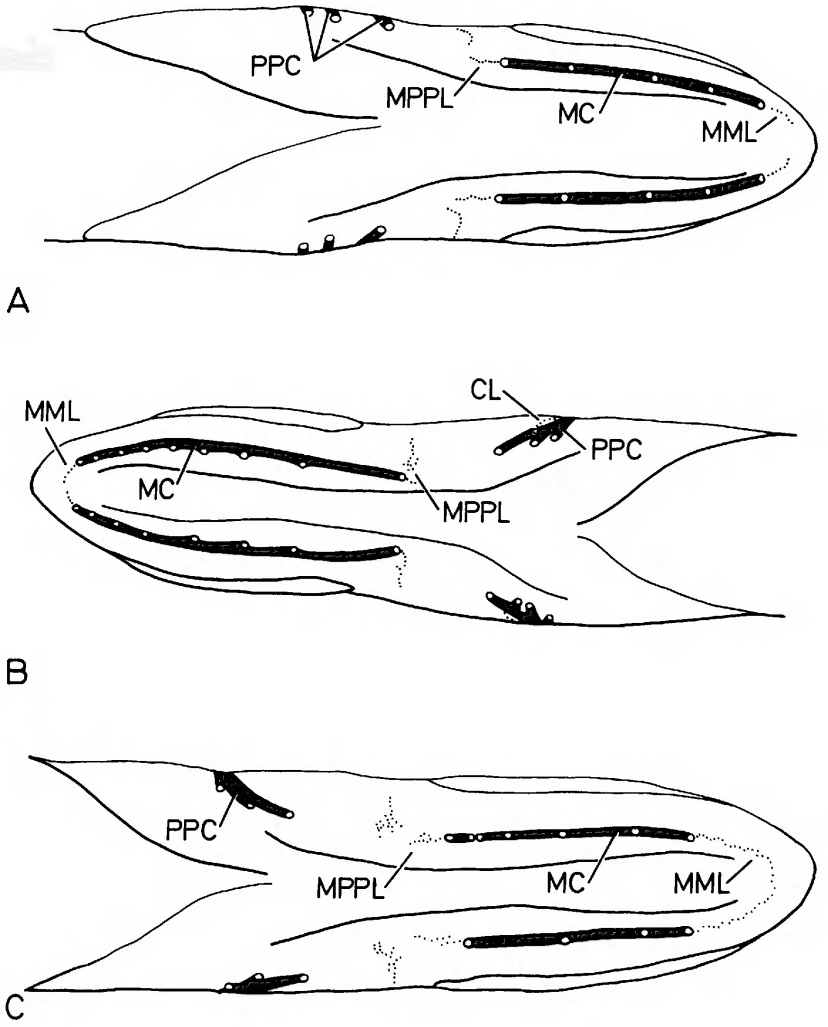


FIG. 5. Cephalic sensory canals, pores, and pitlines, ventral view. A. *Esox lucius*. B. *Esox masquinongy*. C. *Esox americanus "vermiculatus."*

nasal, and opercular pitlines, exact homologues of which are not known to occur in other fishes.

The tendencies toward canal reduction and pitline elaboration have been continued within each of the two esocoid groups. In the pickerels (*Esox americanus*, *E. niger*) the extrascapular canal has been eliminated and the infraorbital canal has been interrupted at two points; where a canal has been eliminated or interrupted, a pitline has been elaborated in its place. In the pikes (*E. lucius*, *E. reicherti*, *E. masquinongy*), in contrast, both

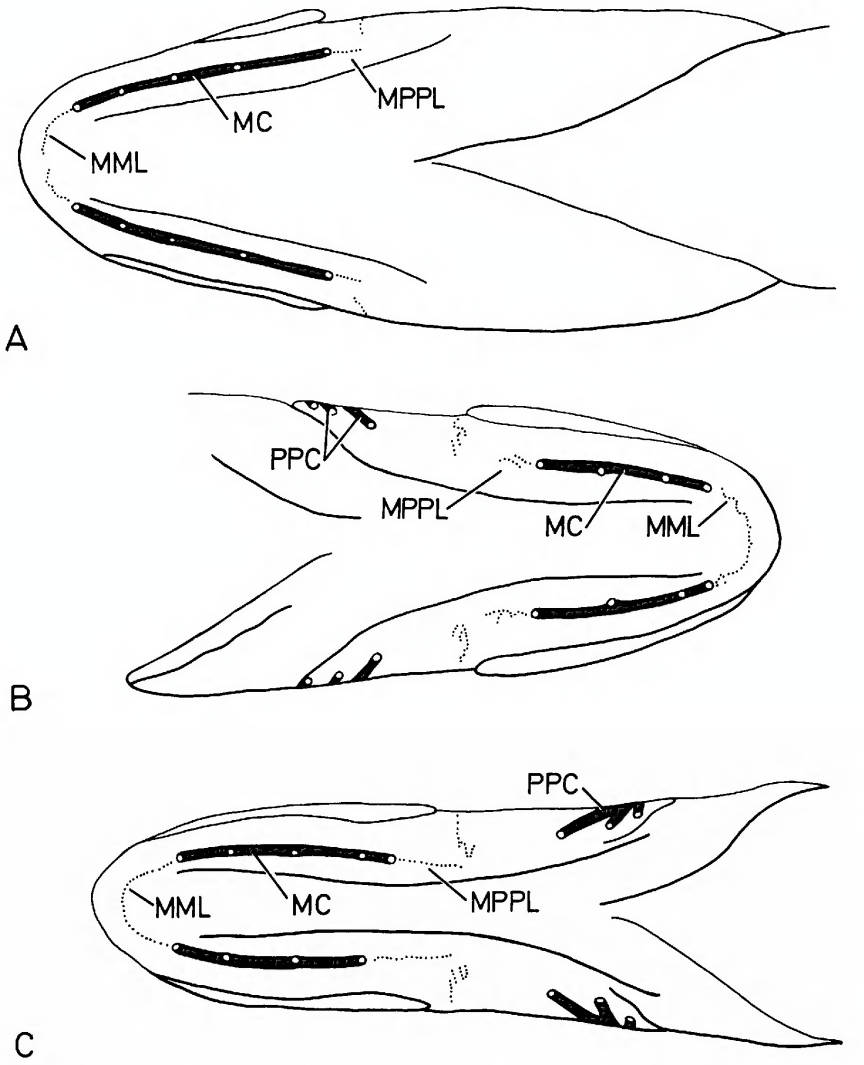


FIG. 6. Cephalic sensory canals, pores, and pitlines, ventral view. A. *Esox reicherti*. B. *Esox americanus "americanus."* C. *Esox niger*.

an extrascapular canal and a complete infraorbital canal have been retained. In *Dallia*, *Umbra limi*, and *U. pygmaea*, the mandibular canal has been eliminated and a pitline elaborated; in *Novumbra* and *U. krameri* a small mandibular canal (two pores) is retained. In *Dallia* and *Umbra* the infraorbital canal has been eliminated posteriorly and the extrascapular canal completely; in *Novumbra* the posterior portion of the infraorbital canal (two pores), and the extrascapular canal (three pores) are retained. Similarly, where a canal has been eliminated, a pitline has been elabo-

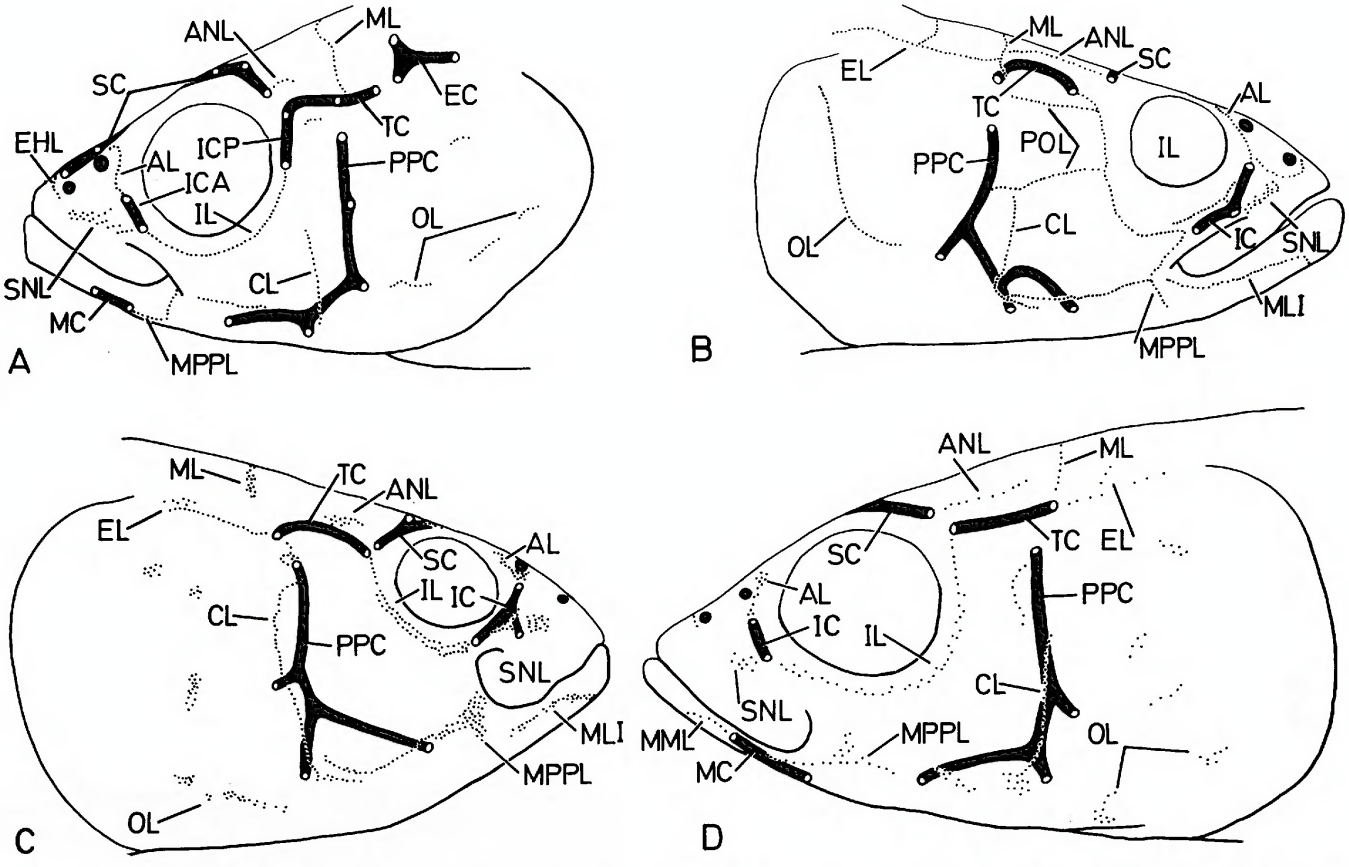


FIG. 7. Cephalic sensory canals, pores, and pitlines, lateral view. A. *Novumbra hubbsi*, UMMZ 187427, 18 mm. B. *Dallia pectoralis*, AMNH 1526, 34 mm. C. *Umbra pygmaea*, AMNH 22745, 25 mm. D. *Umbra krameri*, UMMZ 185076, 13 mm.

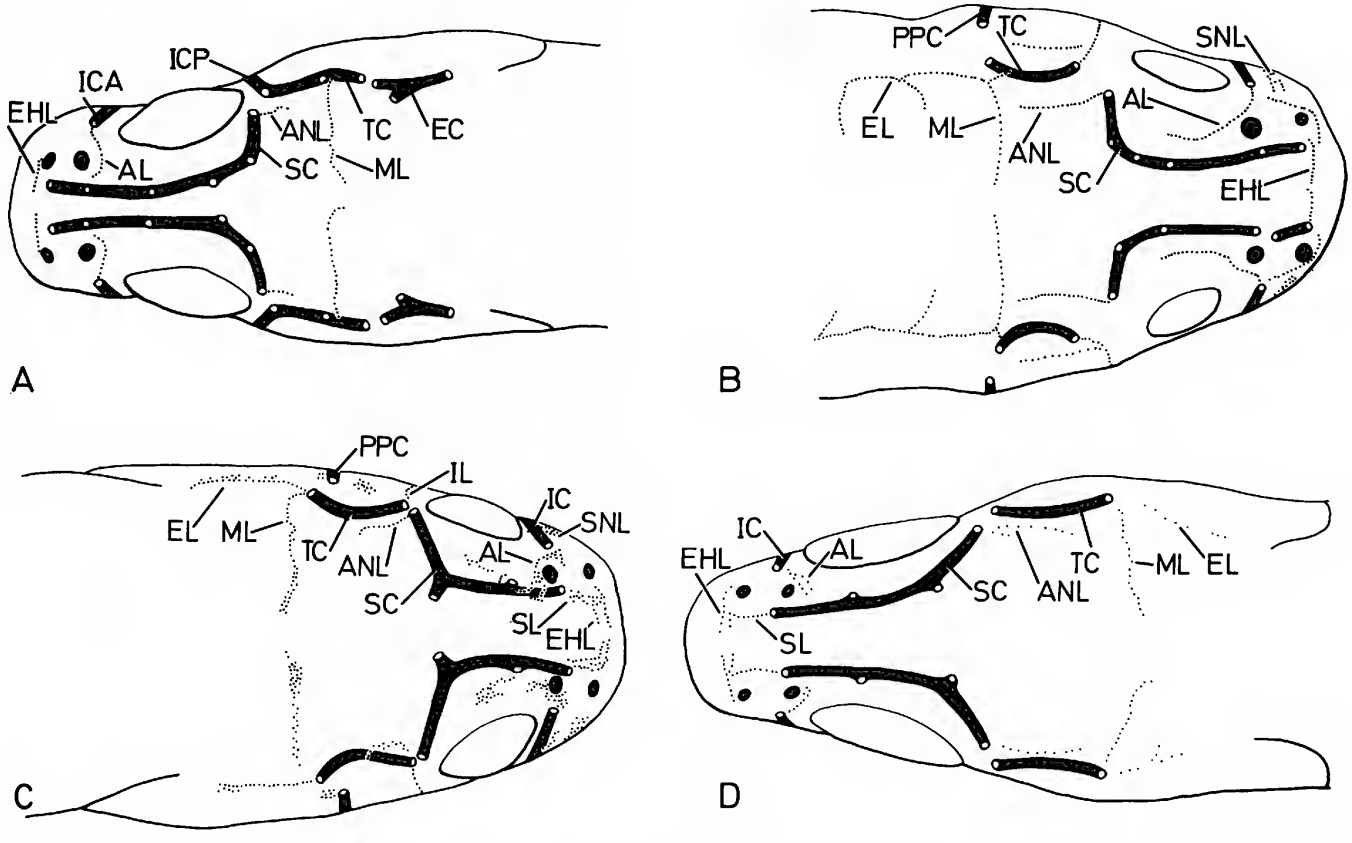


FIG. 8. Cephalic sensory canals, pores, and pitlines, dorsal view. A. *Novumbra hubbsi*. B. *Dallia pectoralis*. C. *Umbra pygmaea*. D. *Umbra krameri*.

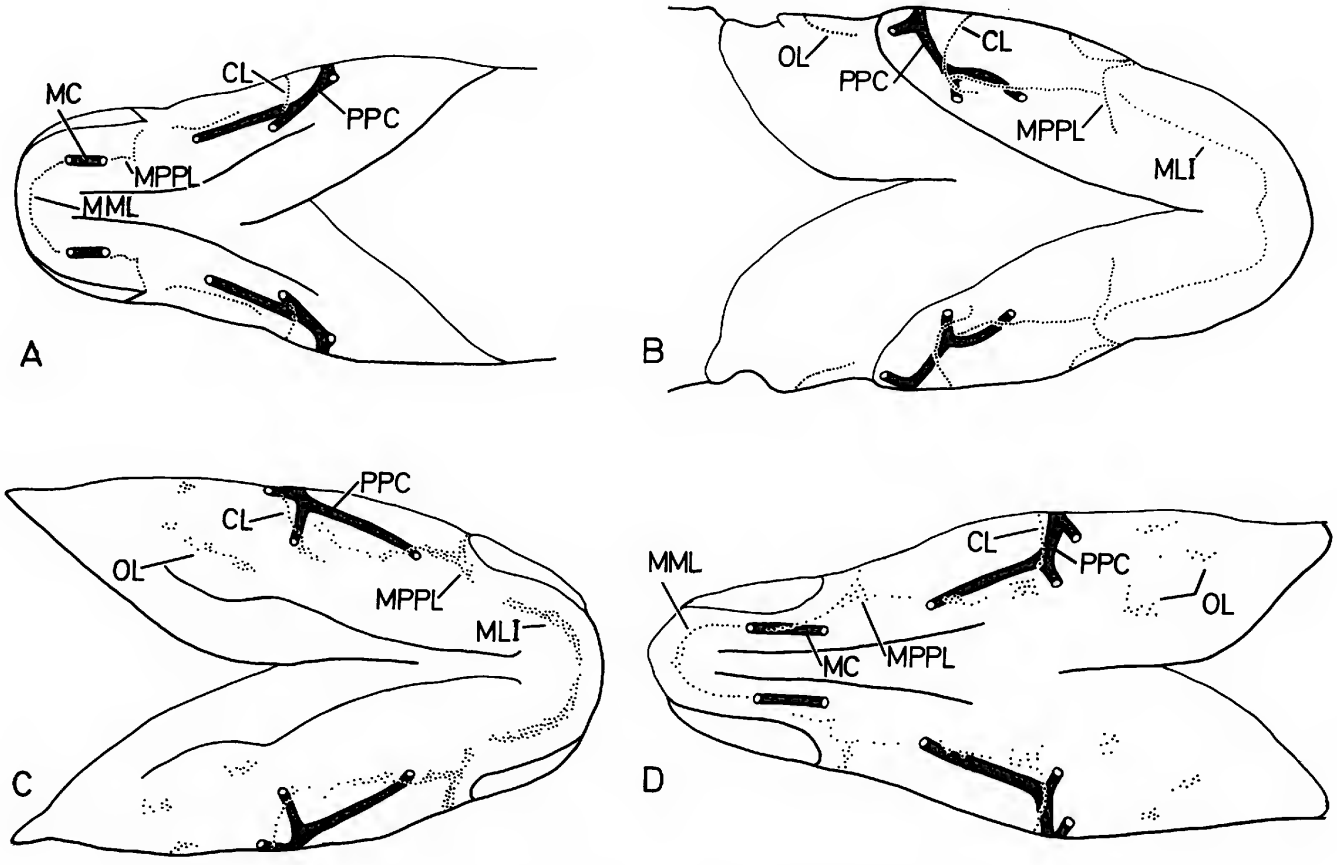


FIG. 9. Cephalic sensory canals, pores, and pitlines, ventral view. A. *Novumbra hubbsi*. B. *Dallia pectoralis*. C. *Umbra pygmaea*. D. *Umbra krameri*.

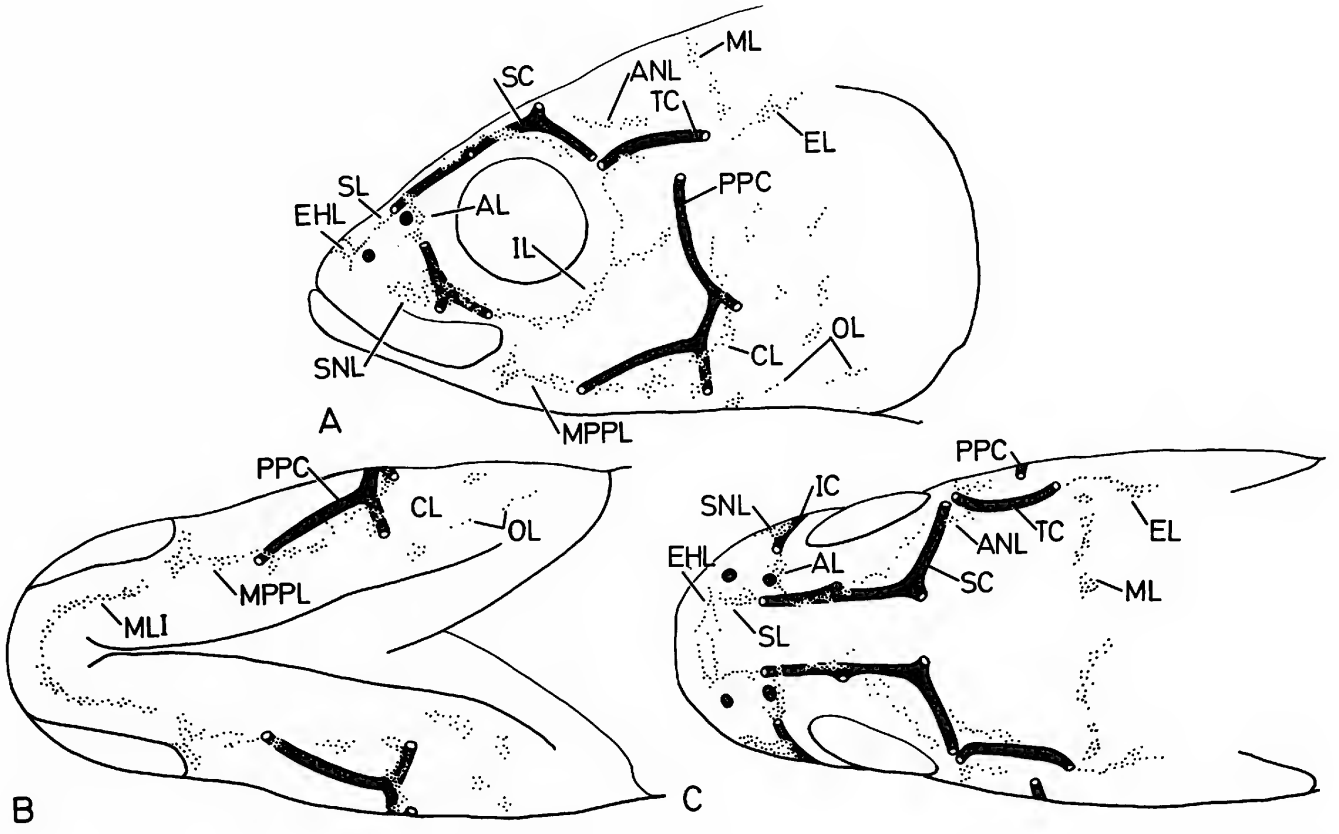


FIG. 10. *Umbra limi*, AMNH 27232, 19 mm., cephalic sensory canals, pores, and pitlines. A. Lateral view. B. Ventral view. C. Dorsal view.

FIG. 11. *Umbra limi*, left side of head, showing sensory pores and pitlines.

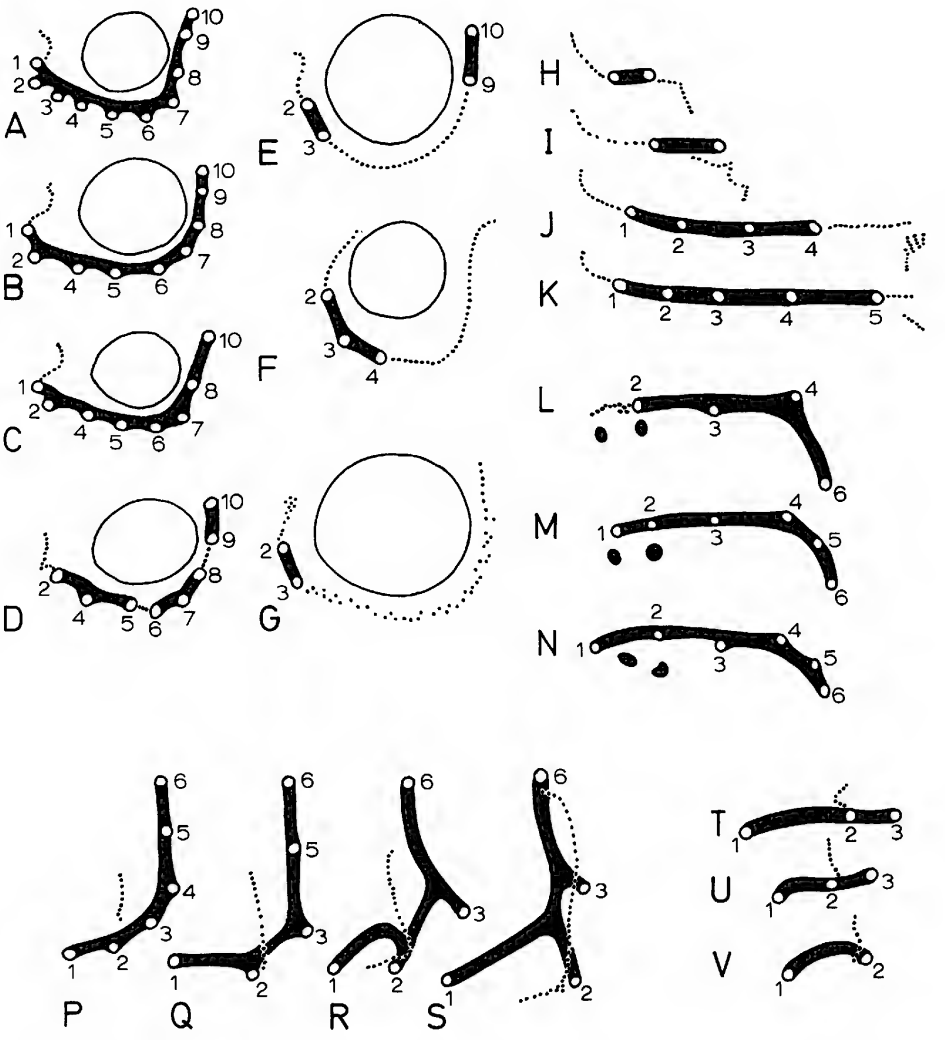


FIG. 12. A–G. Infraorbital canal and associated pores and pitlines, lateral view of left side. A. *Esox masquinongy*. B. *Esox lucius*. C. *Esox reicherti*. D. *Esox americanus "americanus."* E. *Novumbra hubbsi*. F. *Dallia pectoralis*. G. *Umbra krameri*. H–K. Mandibular canal and associated pores and pitlines, ventral view of left side. H. *Novumbra hubbsi*. I. *Umbra krameri*. J. *Esox niger*. K. *Esox reicherti*. L–N. Supraorbital canal and associated pores and pitlines, dorsal view of left side. L. *Umbra limi*. M. *Novumbra hubbsi*. N. *Esox americanus "americanus."* P–S. Preopercular canal and associated pores and pitline. P. *Esox americanus "vermiculatus."* Q. *Novumbra hubbsi*. R. *Dallia pectoralis*. S. *Umbra pygmaea*. T–V. Temporal canal and associated pores and pitline. T. *Esox niger*. U. *Novumbra hubbsi*. V. *Dallia pectoralis*.

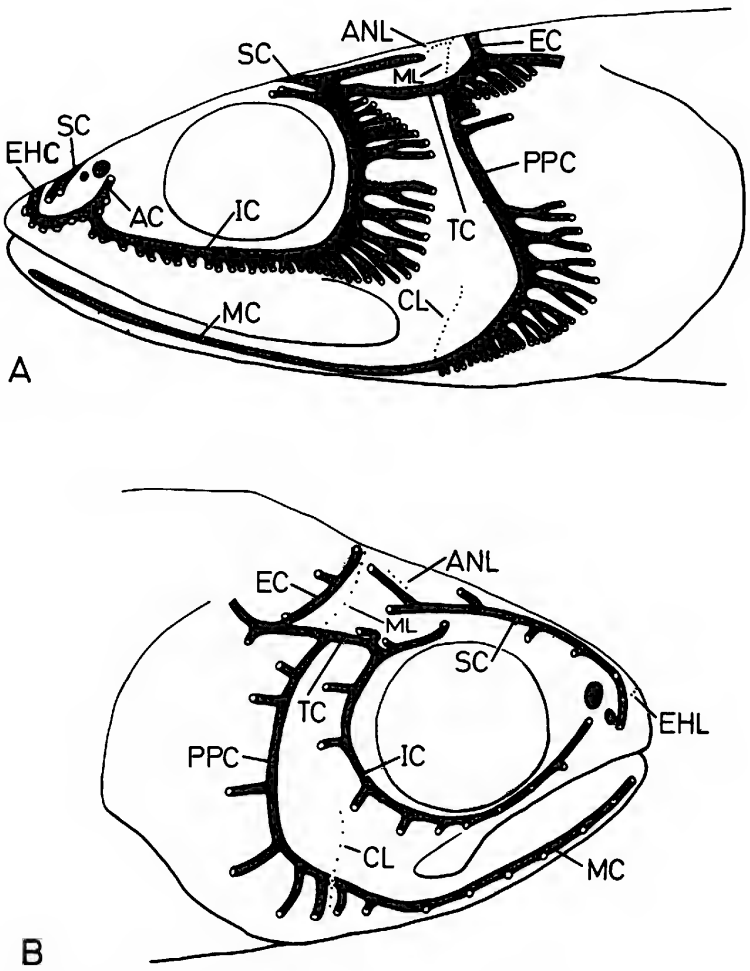


FIG. 13. Cephalic sensory canals, pores, and pitlines, lateral view. A. *Elops hawaiiensis*, AMNH uncatalogued, about 25 mm. (pores and tubes omitted from supraorbital, mandibular, and extrascapular canals). B. *Hiodon alosoides*, AMNH 23754, 17 mm.

rated. Umbrids in general have the mandibular, preopercular, infraorbital, supraorbital, and temporal canals more reduced and the corresponding pitlines better developed than esocids. Pitline elaboration in umbrids in some cases involves not only single, but double lines, more complex bands of organs, and new lines without exact equivalents in other species (the postocular pitlines of *Dallia*, fig. 7B).

Reduction of canals may involve (1) the loss of enclosed canals and pores and the modification of canal neuromasts into superficial pitorgans, or (2) the retention of a canal with fewer pores and neuromasts. In the

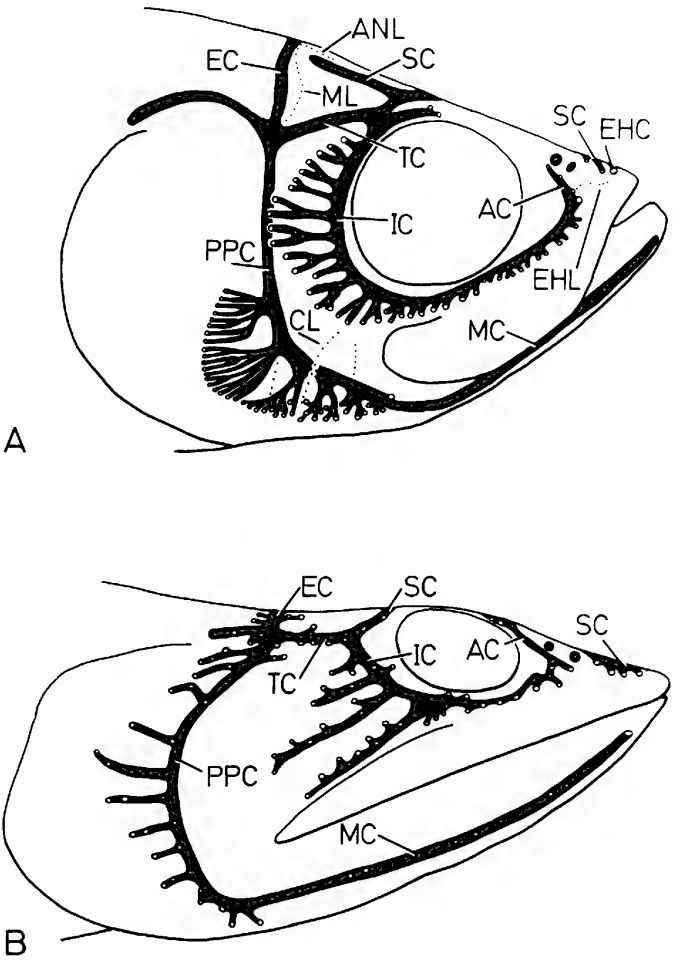


FIG. 14. Cephalic sensory canals, pores, and pitlines, lateral view. A. *Megalops cyprinoides*, AMNH uncatalogued, 23 mm. (pores and tubes omitted from supraorbital, mandibular, and extrascapular canals). B. *Synodus synodus*, AMNH 23344, 29 mm. (pitlines omitted).

laterosensory system in general a primary pore develops between each two successive canal neuromasts (e.g., Allis, 1889). In ontogeny the neuromasts develop first, the pores later, their pattern apparently determined in some way by that of the neuromasts.

INFRAORBITAL CANAL: The infraorbital canal of esocoids may include from two to 10 or more pores. In *Esox lucius*, *E. masquinongy*, and *E. reicherti* the infraorbital canal is continuous, enclosed within a complete infraorbital series of bones (Allis, 1904, fig. 22; Pehrson, 1944, fig. 12; Nelson, 1969c, fig. 9). In *Esox americanus* and *E. niger*, the infraorbital canal is

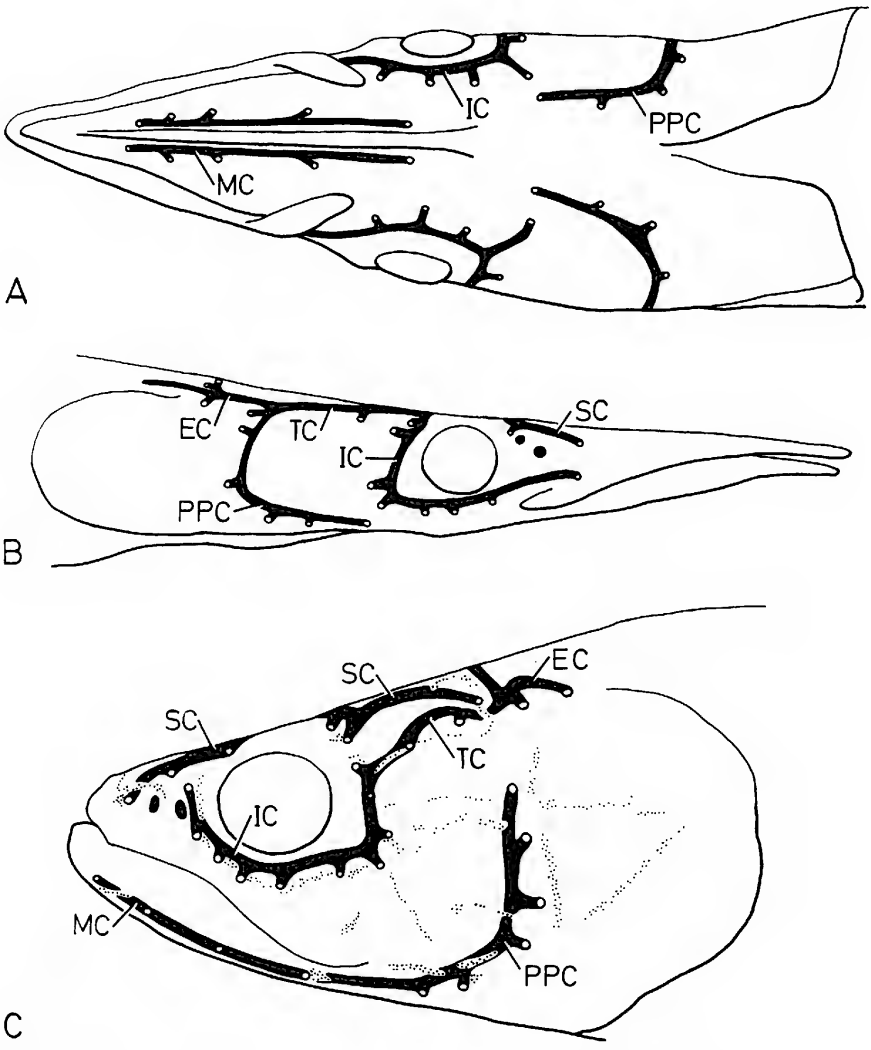


FIG. 15. Cephalic sensory canals, pores, and pitlines. A–B. *Salanx chinensis*, AMNH 10336, 32 mm., ventral and lateral views (pitlines omitted). *Hoplias malabaricus*, AMNH 22736, 34 mm., lateral view.

discontinuous, and the infraorbital series of bones incomplete (Nelson, 1969c, fig. 9), but the number of pores is not significantly reduced. In umbrids the canal is further reduced. The anterior part, as in *E. americanus* and *E. niger*, is enclosed within the lacrimal. In umbrids the posterior part, present only in *Novumbra*, is enclosed within a bone comparable to the fifth or sixth infraorbital of *Esox*. Superficial comparisons between the various pore patterns are possible on the basis of their position (fig. 12A–G)

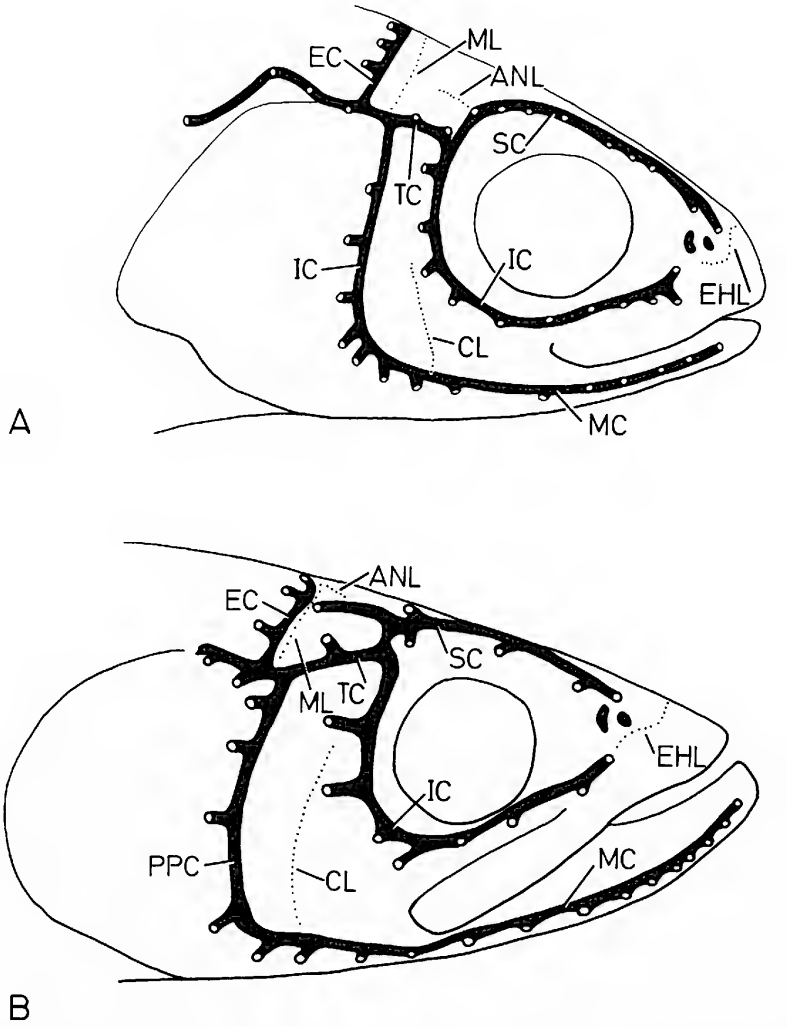


FIG. 16. Cephalic sensory canals, pores, and pitlines, lateral view. A. *Thymallus arcticus*, AMNH 17267, 30 mm. B. *Osmerus mordax*, AMNH 27638, 35 mm.

but detailed homologies will probably be better based on a comparative study including bones and nerves. Apparent, however, is a general trend toward replacement of the infraorbital canal by a pitline, and the modification of canal neuromasts into superficial pitorgans. Where superficial organs occur, they are small and numerous relative to the canal organs they replace.

MANDIBULAR CANAL: The mandibular canal of esocoids may include from two to nine or more pores. In *Esox lucius* and *E. reicherti*, the usual number is five; in *E. americanus* and *E. niger* the usual number is four. A

superficial comparison between the two conditions suggests that in *E. americanus* and *E. niger* a reduction in the posterior part of the canal has occurred, with the elaboration of a pitline (fig. 12H–K). In *Novumbra* and *U. krameri* the mandibular canal includes only two pores, which on a superficial basis can be compared only arbitrarily with those of *Esox*.

SUPRAORBITAL CANAL: The supraorbital canal of esocoids includes from four to six or more pores. In *Esox*, *Novumbra*, and *Dallia* the anterior part of the canal, containing one neuromast, is enclosed within a tubular nasal bone (Cavender, 1969, p. 20). The nasal bone and associated canal and neuromast are absent from *Umbra*, which has instead a pitline representing the anterior part of the supraorbital canal, as shown by its innervation. A superficial comparison of the pore patterns in the remaining part of the canal in *Umbra* suggests a loss of one pore and neuromast from the posterior part of the canal (fig. 12L–N).

PREOPERCULAR CANAL: The preopercular canal of esocoids includes from four to six pores. The cheek pitline is oriented toward the second pore of the series, which may be taken as a point of reference. In *Esox* there are six pores, in *Novumbra* five, and in *Dallia* and *Umbra*, four. A superficial comparison suggests a loss of one pore and neuromast from the ascending part of the canal of *Novumbra*, and a loss of a second pore and neuromast from the same region of the canal of *Dallia* and *Umbra*. In *Umbra* the cheek pitline is deflected posterior to the ascending part of the canal (fig. 12P–S).

TEMPORAL CANAL: The temporal canal of esocoids includes either two or three pores. In *Esox* and *Novumbra* there are three pores. The middle pitline is oriented toward the second pore of the series. A superficial comparison with *Dallia* and *Umbra* suggests a loss of the posterior pore and neuromast from the temporal canal of these genera (fig. 12T–V).

## INTERRELATIONSHIPS AND CLASSIFICATION OF RECENT ESOCOIDS

On the basis of the foregoing comparisons of characters and analysis of phyletic trends, one may construct a theory of the interrelationships of the Recent esocoid species. For this purpose what is important are the characters advanced relative to those primitive for teleosts. These characters, and the monophyletic groups they indicate, are as follows (primitive characters are given in parentheses):

1. Cephalic sensory canals subdivided into mandibular, preopercular, supraorbital, infraorbital, temporal, extrascapular, and posttemporal components sometimes represented by pitlines; ethmoidal and antorbital canals represented by

pitlines; mandibulopreopercular, subnasal, and opercular pitlines present . . . . . suborder Esocoidei
2a. Anterior pitline rudimentary or absent (infraorbital canal with eight or more pores; mandibular canal with four or more pores; opercular canal with six pores; posttemporal canal present) . . . . . family Esocidae, genus *Esox*
3a. Ethmoidal pitline double (infraorbital canal continuous; extrascapular canal present) . . . . . subgenus *Esox*
4a. (Mandibular canal with five pores). . . . . *Esox lucius, E. reicherti*
4b. Mandibular canal with six to nine pores . . . . *Esox masquinongy*
3b. Infraorbital canal discontinuous, interrupted in two places and pitlines elaborated; extrascapular canal absent, represented by a pitline (ethmoidal pitline single). . subgenus *Kenoza* (*Esox americanus, E. niger*)
2b. Infraorbital canal with three or fewer pores, mostly represented by a pitline; mandibular canal with two pores or none; opercular canal with four or five pores; posttemporal canal absent (anterior pitline present) . . . . . family Umbridae
5a. (Infraorbital canal developed posteriorly; extrascapular canal present; preopercular canal with five pores). . . . . subfamily Novumbrinae (*N. hubbsi*)
5b. Infraorbital canal absent posteriorly, represented by a pitline; temporal canal with two pores; extrascapular canal absent, represented by a pitline; preopercular canal with four pores . . . . . subfamily Umbrinae
6a. Postocular pitlines present; mandibular canal absent, represented by a pitline (supraorbital canal with six pores; ethmoidal pitline single, cheek pitline anterior in position) . . . . . genus *Dallia* (*D. pectoralis*)
6b. Supraorbital canal with four pores, but reduced anteriorly, where it is represented by a pitline; ethmoidal pitline double; cheek pitline posterior in position, over or behind opercular canal (postocular pitlines absent; mandibular canal present in one species) . . . . . genus *Umbra*
7a. Infraorbital canal with two pores (mandibular canal with two pores) . . . . . subgenus *Umbra* (*U. krameri*)
7b. Mandibular canal absent, represented by a

pitline (infraorbital canal with three pores) . . . . . subgenus *Melanura* (*U. limi*, *U. pygmaea*)

Some species pairs (*Esox lucius* and *E. reicherti*, *Esox americanus* and *E. niger*, and *Umbra limi* and *U. pygmaea*) have more or less identical patterns of cephalic sensory canals and pitlines, and the species of such pairs cannot be distinguished on the basis of these characters.

For esocids the monophyletic groups indicated are generally the same as those expressed, however implicitly, in current classifications. For umbrids at least one of the monophyletic groups indicated is not embodied in some classifications, which, to one degree or another, tend to isolate *Dallia* in a subfamily, family, or even order of its own. For both esocids and umbrids, however, a nomenclature is available and adequate to denote all the monophyletic groups indicated by the evidence presented here. No new names are proposed or suggested to be either necessary or desirable.

The relationships of *Dallia*, once placed in an order by itself because of its numerous peculiarities (Gill, 1885, p. 728; Jordan, 1887, p. 839; Jordan and Evermann, 1896, p. 620), have been most recently discussed by Cavender. Following Greenwood et al. (1966), he included *Novumbra* and *Dallia* with *Umbra* in a single family Umbridae, but gave no subfamilial classification, apparently in the belief that "the fossil evidence is still too meager to decipher evolutionary lines" and that "the living members are mostly faunal relicts well separated from each other by time and probably also by unknown extinct forms" (Cavender, 1969, p. 23).

He stated, however, that "the original mudminnow group was divided into two phyletic lines represented by an ancestral *Umbra* type and by an ancestral *Novumbra* type from which *Dallia* split off"; and, further, that "*Dallia* appears to be closer to *Novumbra* than to any other living esocoid and could well have shared a common ancestry with *Novumbra*" (Cavender, 1969, p. 23).

This proposed relationship between *Novumbra* and *Dallia* seems due partly to Schultz (1929, p. 2), who found that *Novumbra* "has a pectoral girdle intermediate between that of *Dallia pectoralis* and *Umbra limi*." Schultz did not state the nature of the intermediacy of *Novumbra*, but in his figure of the endoskeletal pectoral girdle (pl. 1, fig. 2), it, like that of *Dallia*, is shown entirely cartilaginous. Examination of alizarin specimens of *Novumbra* (UMMZ 187427) shows, however, ossifications corresponding to the scapula, coracoid, and four actinosts of *Umbra* (see also Chapman, 1934, fig. 8). Both *Novumbra* and *Umbra* have the actinosts ossified and separate, unlike their condition in *Dallia*, in which they are cartilaginous and fused together (Starks, 1904, p. 260; Schultz, 1929, pp. 2–3; personal

## TABLE 1

### Canal Pores and Pitlines of Recent Esocoid Fishes

| Species | MC | PPC | IC | ICA | ICM | ICP | SC | TC | EC | PTC | MML | MLI | MPPL | OL | CL | EHL | SNL | AL | SL | ANL | ML | EL | IL | ILA | ILP | POL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *N. hubbsi* | 2 | 5 | → | 2 | — | 2 | 6 | 3 | 3 | — | + | — | + | + | + | + | + | + | — | + | + | — | + | ← | ← | — |
| *D. pectoralis* | — | 4 | → | 3 | — | — | 6 | 2 | — | — | + | + | + | + | + | + | + | + | — | + | + | + | + | ← | ← | + |
| *U. krameri* | 2 | 4 | → | 2 | — | — | 4 | 2 | — | — | + | — | + | + | + | + | + | + | + | + | + | + | + | ← | ← | — |
| *U. limi* | — | 4 | → | 3 | — | — | 4 | 2 | — | — | + | + | + | + | + | + | + | + | + | + | + | + | + | ← | ← | — |
| *U. pygmaea* | — | 4 | → | 3 | — | — | 4 | 2 | — | — | + | + | + | + | + | + | + | + | + | + | + | + | + | ← | ← | — |
| *E. americanus* | 4 | 6 | → | 3 | 3 | 2 | 6 | 3 | — | 2 | + | — | + | + | + | + | + | + | — | + | + | + | → | + | + | — |
| *E. niger* | 4 | 6 | → | 3 | 3 | 2 | 6 | 3 | — | 2 | + | — | + | + | + | + | + | + | — | — | + | + | → | + | + | — |
| *E. lucius* | 5 | 6 | 8+ | ← | ← | ← | 6 | 3 | 3 | 2 | + | — | + | + | + | + | + | + | — | — | + | — | — | — | — | — |
| *E. reicherti* | 5 | 6 | 8+ | ← | ← | ← | 6 | 3 | 3 | 2 | + | — | + | + | + | + | + | + | — | — | + | — | — | — | — | — |
| *E. masquinongy* | 5+ | 6 | 8+ | ← | ← | ← | 6 | 3 | 3 | 2 | + | — | + | + | + | + | + | + | — | — | + | — | — | — | — | — |

*Symbols*: Pore numbers are modal values with variation not indicated. +, pitline present; —, pitline absent.

observ.). In these respects *Novumbra* is not intermediate, but, like *Umbra*, retains the primitive ossifications in their primitive arrangement.

The proposed relationship between *Novumbra* and *Dallia* is unsupported and, perhaps, unsupportable, because "Several of the characters that *Dallia* and *Novumbra* share seem to be primitive for the mudminnow group" (Cavender, 1969, p. 22); indeed, among the characters discussed by

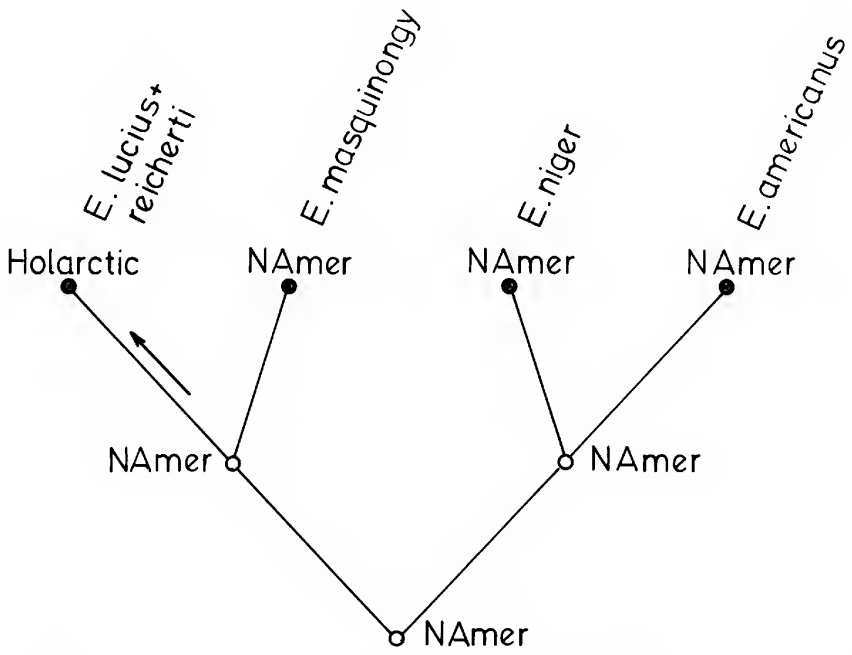


FIG. 17. One possible interpretation of the relationships and geography of esocid fishes. Black circles represent Recent species; white circles, hypothetical ancestral species; the arrow represents a hypothetical expansion of range.

Cavender there are few if any that are unequivocally advanced and shared by *Novumbra* and *Dallia*. For example, Cavender assumed that a low vertebral number, such as that of *Umbra* (32–37) is primitive. Another interpretation is possible, and apparently, preferable (see below): that the high vertebral number of *Novumbra* and *Dallia* (37–42) is primitive.

In his discussion of the relationships of *Novumbra*, Cavender (p. 17), like Schultz (1929), found *Novumbra* "intermediate if not closer to *Dallia* than to *Umbra*." This condition of intermediacy is certainly true for some characters: numbers of pectoral fin rays, vertebrae, and branchiostegal rays. Yet for some of the characters discussed by Cavender (number of principle caudal rays and hypurals, basibranchial dentition, and form of

gillrakers and otoliths), it is *Dallia* that is intermediate between a relatively primitive *Novumbra*-type and a relatively advanced *Umbra*-type. The only advanced character seemingly shared by *Novumbra* and *Dallia* is a relatively high number of pectoral rays, but the difference in ray number is great (table 2). The balance of the advanced characters are shared by *Dallia* and *Umbra*, and seem sufficient to suggest a close relationship between the two genera.

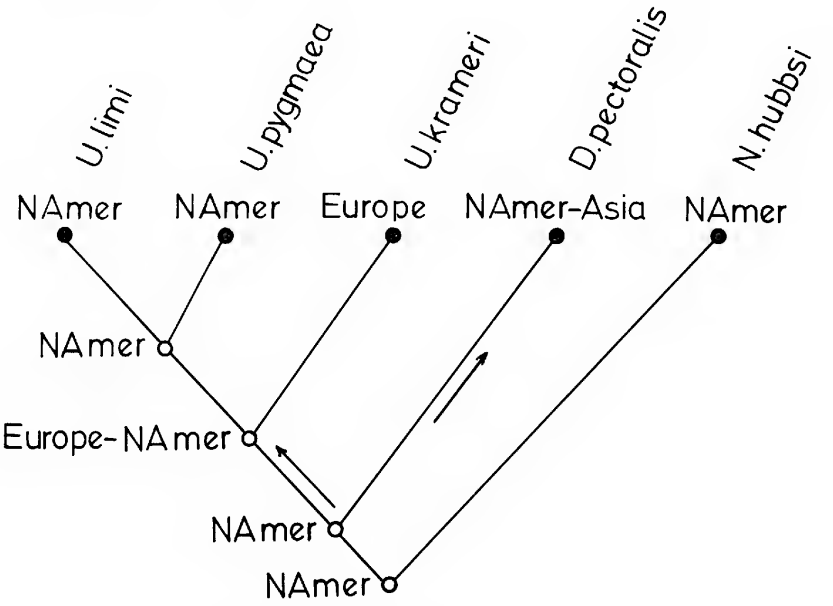


FIG. 18. One possible interpretation of the relationships and geography of umbrid fishes (for explanation see fig. 17).

The results of the present study of the cephalic sensory canals and pitlines are that *Dallia*, aside from its individual peculiarities, shares advanced characters only with *Umbra* (table 1: mandibular canal reduced; four preopercular pores; posterior infraorbital canal reduced; two temporal pores; no extrascapular canal; mandibular and extrascapular pitlines present). These results tend to confirm that *Dallia* is more closely related to *Umbra* than to *Novumbra*. Accordingly, the family Umbridae may be divided into two monophyletic subfamilies, Novumbrinae (including *Novumbra*) and Umbrinae (including *Dallia* and *Umbra*).

## FOSSIL ESOCOIDS

Fossil esocoids, including material previously undescribed, have been most recently dealt with by Sytchevskaya (1968), Cavender (1969),

Cavender, Lundberg, and Wilson (1970), and Crossman and Harington (1970). Most of the fossils have been attributed to Recent genera, but some have been given their own specific names. There is a series of fossil "species" of Esocidae (*Esox destructus*, *E. lepidotus*, *E. otto*, *E. papyraceus*, *E. robustus*, *E. waltschanus*), all European, of various ages (Oligocene, Miocene, Pleistocene). The status and relationships of the fossil European "species" have never been determined; some of them may represent *Esox lucius* (Berg, 1936, p. 391; Crossman and Harington, 1970, p. 1136; see below), known also from various Pleistocene localities in the Holarctic Region (e.g., Pawlowska, 1963; Weiler, 1965). There are some North American esocid fossils (Miocene, Pliocene, Pleistocene), all either attributed to Recent species (*Esox lucius*, *E. masquinongy*) or simply undesignated specifically. There are some North American umbrid fossils attributed to Recent monotypic genera (the Oligocene *Novumbra oregonensis* and the Miocene "*Dallia* sp."), and some European umbrid fossils (the lower Oligocene *Umbra walteri* [mainly otoliths] and the Pliocene *Umbra praekrameri* [otoliths]) attributed to *Umbra*. Collectively, these fossil occurrences indicate that the individual lineages leading to some of the Recent species extend back to Oligocene times. The fossils generally occur in the same areas as the Recent genera or species to which they have been attributed, or to which they are related (excepting minor variations in distribution due presumably to the varying climate of the Pleistocene). In general morphology, the fossils are about the same, so far as is known, as the Recent forms. In addition, there are two monotypic genera described only from fossils, the Middle Eocene *Palaeoesox* from Germany, and the Upper Oligocene *Proumbra* from western Siberia (see below).

Few "characters," other than vertebral number and time of occurrence, have been used to assess the "relationships" of fossil esocoids. A review of the stratigraphic distribution of the fossils shows that older fossils tend to have fewer numbers of vertebrae, and the fossils, stratigraphically arranged, have sometimes been accepted as an ancestor-descendant series (e.g., Berg, 1936; Nikolskii 1950, 1954, 1961). To do so, with the implication that the vertebral number of the oldest fossil is the number most primitive for the group, is an unacceptable substitute for a comparative study (e.g., Schaeffer, Hecht, and Eldredge, MS).

Assuming the relationships of Recent esocoids to be as shown (figs. 17–18, see also table 2), one may construct a hypothesis of the vertebral number for the ancestral species of each monophyletic group: subgenus *Esox* 57–64; subgenus *Kenoza* 43–51; genus *Esox* 43–51; subgenus *Melanura* 32–36; genus *Umbra* 32–36; subfamily Umbrinae 40–42; family Umbridae 40–42. Accepting these estimates, one may theorize that during esocoid evolution,

there has been a tendency to increase vertebral number in the subgenus *Esox* (particularly apparent in *E. masquinongy*) and a tendency to decrease it in the genus *Umbra*.

Turning to the vertebral numbers of fossil species, one notes a low number (33–34) in *Palaeoesox* (Voigt, 1934) and *Proumbra* (Sytchevskaya, 1968), a somewhat higher number (38–39) in *Novumbra oregonensis* (Cavender, 1969), a moderate number (48–51) in *Esox papyraceus*, *E. robustus*, and *E. waltschanus* (Berg, 1936), and a high number (60) in *Esox lepidotus* (Berg, 1936). Vertebral numbers, therefore, indicate that *Palaeoesox* and *Proumbra* are closely related to, and may be members of, the genus *Umbra* (but see below), that *Novumbra oregonensis* is not significantly different from *Novumbra hubbsi*, and that *Esox lepidotus* is closely related to, and may be a member of, the subgenus *Esox*. The relationships of the other fossil esocids (*Esox papyraceus*, *E. robustus*, and *E. waltschanus*) are relatively obscure, for their moderate vertebral number is a character apparently primitive for the subgenus *Kenoza*, the genus *Esox*, and perhaps for the suborder Esocoidei as a whole (possible esocoid relatives are to be found in the suborder Salmonoidei, where vertebral number is generally in excess of 40; see e.g., Cohen, 1964; Frankenberg, MS; McAllister, 1963; McDowall, 1970, 1971; Nielsen and Larsen, 1968; Norden, 1961; Okada, 1959–1960; Stokell, 1941, 1969). About all that can be said on the basis of vertebral number is that *Esox papyraceus*, *E. robustus*, and *E. waltschanus* are probably not closely related to any single species of the subgenus *Esox*; they may, however, form an early sidebranch of the subgenus, or belong to the subgenus *Kenoza*, or to an extinct subgenus of their own.

*Proumbra*, from the Upper Oligocene of western Siberia, has been considered a morphological intermediate between *Dallia*, on the one hand, and *Novumbra* and *Umbra*, on the other. Like *Dallia*, *Proumbra* is said to have ribs on the first vertebra, pelvic fins with less than six rays, and dorsal and anal fins on the posterior third of the body (Sytchevskaya, 1968).

*Dallia pectoralis* is the only Recent esocoid with Baudelot's ligament ossified (personal observ.), and the ossified ligament has sometimes been considered a first rib (Starks, 1904; Chapman, 1934, p. 401; Cavender, 1969, p. 18). In *Dallia* it is well developed, extending from the first vertebra to the pectoral girdle; in *Proumbra* the first ribs are said to be shorter than the second and third pairs, which in turn are shorter than those more posterior; in *Umbra* Baudelot's ligament is unossified and the first vertebra has a prominent transverse process. In *Dallia* the number of pelvic rays is usually three; in *Proumbra* the described number is five; in *Umbra* the number is usually six with five a rare variant (table 2). In *Dallia*, both the predorsal and preanal distances are about 70 per cent of standard length;

TABLE 2

FIN RAYS, LATERAL SCALES, BRANCHIOSTEGAL RAYS, AND VERTEBRAE OF ESOCOID FISHES[a]

| Species | Anal Rays | Dorsal Rays | Pectoral Rays | Pelvic Rays | Caudal Rays | Branched Caudal Rays | Lateral Scales | Branchiostegal Rays | Vertebrae |
|---|---|---|---|---|---|---|---|---|---|
| *N. hubbsi* | 11–13 | 12–15 | 18–23 | 6–7 | 33–34 | 16 | 52–58 | 6–7 | 37–40 |
| *D. pectoralis* | 12–16 | 10–14 | 32–37 | 0–3 | 30+ | 15–16 | 76–100 | 7–9 | 40–42 |
| *U. krameri* | 7–8 | 15–17 | 11–14 | 6–7 | 20 | 8–9 | 30–36 | ? | 32–36 |
| *U. limi* | 8–10 | 14–15 | 14–16 | 6 | 20 | 11 | 35 | 4–5 | 36–37 |
| *U. pygmaea* | 7–10 | 13–16 | 13–14 | 5–6 | 21 | 10–12 | 35 | 4–6 | 33–35 |
| †*P. fritzschei* | 8–9 | 11–13 | 15–17 | 6–7 | ? | ? | 60+ | ? | 33–34 |
| †*P. irtyshensis* | 10–11 | 14–15 | 11 | 5 | 22–23 | 11 | 35–40 | 6 | 33–34 |
| *E. americanus* | 14–20 | 16–21 | 13–16 | 8–10 | 40–44 | 17 | 87–117 | 9–16 | 43–51 |
| *E. niger* | 16–19 | 20–21 | 11–13 | 9–10 | 43–46 | 17 | 112–135 | 14–17 | 50–54 |
| *E. lucius* | 14–21 | 17–25 | 14–17 | 10–11 | 47–50 | 17 | 105–148 | 13–16 | 57–64 |
| *E. reicherti* | 15–18 | 17–22 | 12–17 | ? | ? | ? | 130–156 | 13–14 | 63 |
| *E. masquinongy* | 20–21 | 21–23 | 15–17 | 10–13 | 43–46 | 17 | 140–176 | 16–20 | 63–67 |

[a]Counts are based on Bănărescu (1964), Berg (1948, 1962), Cavender (1969), Chapman (1934), Crossman (1960, 1966), Crossman and Buss (1965), Dick (1964), Jordan and Evermann (1896), McAllister (1968), McPhail and Lindsey (1970), Monod (1968), Nikolskii (1956), Schultz (1929), Smith-Vaniz (1968), Sytchevskaya (1968), Voigt (1934), and personal observations. Variation is indicated where known.

in *Proumbra* they are described as 67–70 per cent and 78–82 per cent, respectively; in *Umbra* they are about 60 percent and 70 per cent, respectively. It is moot whether any of these three characters can be interpreted as advanced and shared by *Dallia* and *Proumbra*. In contrast, *Proumbra* and *Umbra* share some advanced characters: low numbers of anal and caudal rays, lateral scales, vertebrae and branchiostegal rays (table 2). These characters are sufficient to suggest that *Proumbra* is more closely related to *Umbra* than to any other Recent esocoids. *Proumbra* may be tentatively recognized as an extinct subgenus of *Umbra*, but its relationships to the two Recent subgenera remain to be clarified. *Umbra* (*Proumbra*) *irtyshensis* accordingly rests *incertae sedis* (see below).

The oldest fossil esocoid is *Palaeoesox fritzschei* from the Middle Eocene of Germany (Andrews et al., 1967, p. 658). Considered on ancestral esocid by Voigt (1934, see also Nikolskii, 1950, p. 178; 1954, p. 188; 1961, p. 218; Crossman and Harington, 1970, p. 1135), *Palaeoesox* was subsequently placed in its own family by Berg, who stated, however, that *Palaeoesox* "belongs, it is true, to the same division as Umbra" (1936, p. 390). He later grouped the families Umbridae and Palaeoesocidae in a superfamily Umbroidae, which, together with the superfamilies Dallioidae and Esocoidae, constituted his suborder Esocoidei (Berg, 1936; 1940, pp. 242, 429; 1948; 1958; 1962). Cavender (1969, p. 17) also reviewed the relationships of *Palaeoesox* and concluded that it has "a closer relationship to the Umbridae than to the Esocidae."

For the purpose of reviewing the systematic position of *Palaeoesox*, the writer was able to borrow two specimens, of some "500" present in the Geiseltalmuseum, Halle-Wittenberg (Matthes, *in litt.*). In these specimens it was possible to observe parts of the lower jaw and caudal skeleton. Like umbrids, *Palaeoesox* (fig. 19) has a lower jaw with a shallow anterior part, and a deep posterior part which encloses the mandibular sensory canal (Cavender, 1969, fig. 5J, K). As in umbrids the canal, if it was present at all, was probably short with perhaps two pores. In its caudal skeleton, *Palaeoesox* (fig. 20) has six hypurals (two lower and four upper), the lower large and the upper small, with some gradation in size (see also Voigt, 1934, pl. 3, fig. 4). As in *Dallia* (Monod, 1968, fig. 445; Cavender, 1969, fig. 6) and *Umbra* (Breder, 1933, fig. 2; Dineen and Stokely, 1954, fig. 2; Greenwood et al., 1966, fig. 4B; Monod, 1968, fig. 447), the first hypural of *Palaeoesox* is not significantly larger than the others, and there is no gap between the lower and upper hypurals in contrast to the condition (presumably primitive for esocoids) of *Novumbra* (Chapman, 1934, fig. 6; Cavender, 1969, p. 19) and esocids (Gosline, 1960, fig. 3; Monod, 1968,

FIG. 19. *Palaeoesox fritzschei*, MLU uncatalogued, cranial skeleton, ventrolateral view (total length about 65 mm.).

FIG. 20. *Palaeoesox fritzschei*, MLU C-70, caudal skeleton, lateral view of right side (total length about 70 mm.).

fig. 443). As in Recent umbrids, *Palaeoesox* probably had a round rather than a forked tail.

If *Novumbra*, *Dallia*, and *Umbra* are all related more closely to each other than to esocids, they may be included in a single family, Umbridae, coordinate with the Esocidae (Berg, 1931). If so, *Palaeoesox* should be included in the Umbridae. But its relationships within the family are not yet clear. *Palaeoesox* shares some advanced characters with *Umbra* (Cavender, 1969, p. 16; and above), and it is possible that *Palaeoesox* really is an *Umbra* or perhaps an umbrine. Voigt (1934), however, has described for *Palaeoesox* numerous (14) branchiostegal rays and a complete series of infraorbital bones; these are characters of esocids and, ultimately, characters primitive for esocoids as a whole, but not present in any Recent umbrid. If their presence in *Palaeoesox* were confirmed (branchiostegal and infraorbital characters of fossils have often been inaccurately observed), there would be some reason to suggest that *Novumbra*, *Dallia*, and *Umbra* are more closely related among themselves than they are to *Palaeoesox*, and that *Palaeoesox* should be placed in an extinct subfamily of its own. At present, however, *Palaeoesox* can rest only *incertae sedis* within the Umbridae (see below).

## A CLASSIFICATION OF FOSSIL AND RECENT ESOCOID FISHES

Suborder Esocoidei Berg, 1936
- Family Esocidae Cuvier, 1817
  - Genus *Esox* Linnaeus, 1758
    - Subgenus *Esox* Linnaeus, 1758
      - Species *Esox lucius* Linnaeus, 1758
      - Species *Esox masquinongy* Mitchill, 1824[1]
    - Subgenus *Esox*, *incertae sedis*
      - †Species *Esox lepidotus* Agassiz, 1832
      - Species *Esox reicherti* Dybowski, 1869
    - Subgenus *Kenoza* Jordan and Evermann, 1896
      - Species *Esox americanus* Gmelin, 1788
      - Species *Esox niger* Lesueur, 1818
- Family Esocidae, *incertae sedis*
  - †Species *Esox destructus* Laube, 1901
  - †Species *Esox otto* Agassiz, 1843
  - †Species *Esox papyraceus* Troschel, 1854
  - †Species *Esox robustus* Winkler, 1861
  - †Species *Esox waltschanus* Meyer, 1848
- Family Umbridae Günther, 1866

[1] The synonymy and an account of the unsuccessful search for the original description are being treated elsewhere by E. J. Crossman (personal communication). The citation "Mitchill, 1824" follows the traditional usage dating from DeKay (1842, pp. 222–223).

Subfamily Novumbrinae Schultz, 1929
Genus *Novumbra* Schultz, 1929
†Species *Novumbra oregonensis* Cavender, 1969
Species *Novumbra hubbsi* Schultz, 1929
Subfamily Umbrinae Günther, 1866
Genus *Dallia* Bean, 1880
Species *Dallia pectoralis* Bean, 1880
Genus *Umbra* Walbaum, 1792[1]
Subgenus *Melanura* Agassiz, 1853
Species *Umbra limi* (Kirtland, 1841)
Species *Umbra pygmaea* (DeKay, 1842)
Subgenus *Umbra* Walbaum, 1792
Species *Umbra krameri* Walbaum, 1792[2]
Genus *Umbra, incertae sedis*
†Subgenus *Proumbra* Sytchevskaya, 1968
†Species *Umbra irtyshensis* Sytchevskaya, 1968
Family Umbridae, *incertae sedis*
†Species *Umbra praekrameri* Weinfurter, 1950
†Species *Umbra weileri* Martini, 1965
†Genus *Palaeoesox* Voigt, 1934
†Species *Palaeoesox fritzschei* Voigt, 1934

## ESOCOID GEOGRAPHY

Esocoids, both fossil and Recent, are known natively only from the Holarctic Region, and are considered primary freshwater fishes in the sense of Myers (1938), e.g., by Beaufort (1951), Darlington (1957), and Bănărescu (1970). Of the five Recent species of esocids, *Esox lucius* is itself Holarctic in distribution, *E. reicherti* is east Asian (Amur Basin), and *E. americanus*, *E. masquinongy*, and *E. niger* are central and east North American. Of the five Recent species of umbrids, *Umbra krameri* is southeast European (Romania and adjacent countries), *Dallia pectoralis* is northeast Asian (Siberia) and northwest North American (Alaska), *Novumbra hubbsi* is northwest North American (Washington), and *Umbra limi* and *U. pygmaea* are central and east North American (for distributions of Recent species see Bănărescu, 1964; Berg, 1934, 1948; 1962; Hubbs and Lagler, 1958; McPhail, 1967; McPhail and Lindsey, 1970; Miller 1958; Nikolskii, 1956; Pflieger, 1971: Trautman, 1957; Walters 1955; Wheeler, 1969; for

[1] The authorship of the generic name "*Umbra*" is sometimes attributed to Scopoli, e.g., by Martini (1965, p. 310; see also Gill, 1903, p. 296). The citation "Walbaum, 1792" follows Berg (1962, p. 483).

[2] The nomenclature of the European *Umbra* is unsettled, according to E. J. Crossman (in Beamish, Merrilees, and Crossman, 1971). The name "*Umbra krameri*" follows Berg (1962, p. 484).

stratigraphic and geographic distributions of fossil species, Sytchevskaya, 1968; Cavender et al., 1970; Crossman and Harington, 1970). Their distribution has been either viewed as problematical (e.g., Beaufort, 1951, p. 37), or interpreted in relation to a supposed North American origin (Bănărescu, 1960, p. 57), or to a supposed Eurasian origin, by way of an "ancestral" *Palaeoesox*, and "migration" into North America, by way of a "Bering land bridge" (Darlington, 1957, pp. 33–34; Crossman and Harington, 1970).

For a historical geographical analysis, it is neither necessary nor desirable to make assumptions of ancestor-descendant relationships for they necessarily bias the results (Nelson, 1969b, 1970b). For example, if (1) *Palaeoesox* is not assumed to be an ancestral esocoid but simply an umbrid, perhaps even an *Umbra* closely related to *U. krameri*; (2) *Esox lepidotus* is not assumed to be ancestral but only closely related to, or perhaps conspecific with, *Esox lucius*; and (3) the *papyraceus-waltschanus* complex is not assumed to be ancestral to other forms, but closely related to, or a member of, the subgenus *Kenoza*, a hypothesized North American origin of the Umbridae, Esocidae, and Esocoidei would be consistent with a most parsimonious theory (figs. 17–18). The European esocoids would then emerge as offshoots of a primitively North American fauna involving two European-east North American distributions (*Umbra* and *Kenoza*) and one (*Esox lucius*) Holarctic distribution.

One might hypothesize that all three involved an old (pre-Miocene) faunal connection across what is now the North Atlantic Ocean. An Asian-west North American distribution is, of course, manifested by the Recent species *Dallia pectoralis*, and a "Bering land bridge" of fairly recent date is, perhaps, involved. *Dallia* is known from islands (St. Lawrence, St. Matthew, and Nunivak) in the Bering Sea (McPhail and Lindsey, 1970, p. 214).

With respect to historical interpretations of biogeography, alternative hypotheses are possible. For example, the phyletic relationship between the North American and European *Umbra* may be well established. That it is a transatlantic rather than a transpacific relationship is, however, a matter of interpretation, ultimately depending upon a criterion of parsimony — a minimum distance "track" (Croizat, 1952, p. 9; 1958; 1962, p. 7; 1965, p. 60; 1968a, p. 142; 1968b, p. 47; 1968c, p. 556; 1969, p. 111; 1970, p. 258), "tree" (Edwards and Cavalli-Sforza, 1964, fig. 1), or phylogenetic diagram (Hennig, 1960, 1966; Brundin, 1966), interconnecting the known geographical distributions of the known species, both fossil and Recent. The writer hopes elsewhere to consider further implications of this criterion for the erection of such hypothetical channels

(tracks) of dispersal (see also Nelson, 1969b, 1969c).

An opportunity to test a particular interpretation arises when a previously unknown species of the group is discovered. *Proumbra* may offer such an opportunity. The interpretation to be tested is the track of the subfamily Umbrinae (*Dallia* and *Umbra*). The track may be considered to extend either from (1) east Siberia-Alaska across North America to east North America-Europe (e.g., Bănărescu, 1960), or from (2) east Siberia-Alaska across Eurasia to east North America-Europe (e.g., Jakovlev, 1961). The occurrence of *Proumbra* east of the Urals (Irtysh Basin) accords better with alternative (2), assuming that *Proumbra* is related to (i.e., is the sister group of) *Umbra* rather than *Dallia* (in order to account for *Proumbra*, alternative (1) would require a North American-west Siberian relationship, i.e., a significant parallel dispersal). If so, the Umbridae may still be primitively North American (west North American), but the distribution of *Umbra* in east North America may be secondary. The validity of this conclusion depends, of course, on the precise nature of the interrelationships of *Proumbra* and the Recent species of *Umbra* — which remains to be clarified.

What might be emphasized, however, is that the status and relationships of the Recent and fossil species require precise understanding before they can contribute much to a geographical discussion. The *Esox lucius* complex of populations, of which the "species" *Esox reicherti* might be a part, itself requires precise analysis (e.g., Morrow, 1964). The relationships of all the fossil species remain relatively obscure and in need of further study; nothing can be gained by regarding them as primitive forms ancestral to other species simply because they are fossilized and occur earlier. Without further knowledge of the interrelationships of Recent and fossil esocoids further discussion of their historical geography, except in relation to that of the northern biota as a whole, seems pointless.

## COMPARISON OF ESOCOID WITH GALAXIID FISHES

Like esocoids, galaxiid fishes have the cephalic sensory system subdivided into separate canals: mandibular, preopercular, supraorbital, infraorbital, and temporal. Three basic patterns are apparent: (1) in *Prototroctes*, *Retropinna*, and *Stokellia* (figs. 21A, 22A), all canal components are present, and the infraorbital canal is in two parts, anterior and posterior; (2) in *Aplochiton*, *Brachygalaxias*, *Galaxias*, *Lovettia*, *Neochanna*, and *Nesogalaxias* (figs. 21B, 22B) there is neither a temporal nor a posterior part of an infraorbital canal; (3) in *Lepidogalaxias*, a benthic form (Mees, 1961; Frankenberg, MS; personal observ.), a preopercular canal (three pores) is present but all others are absent (Frankenberg, MS; personal

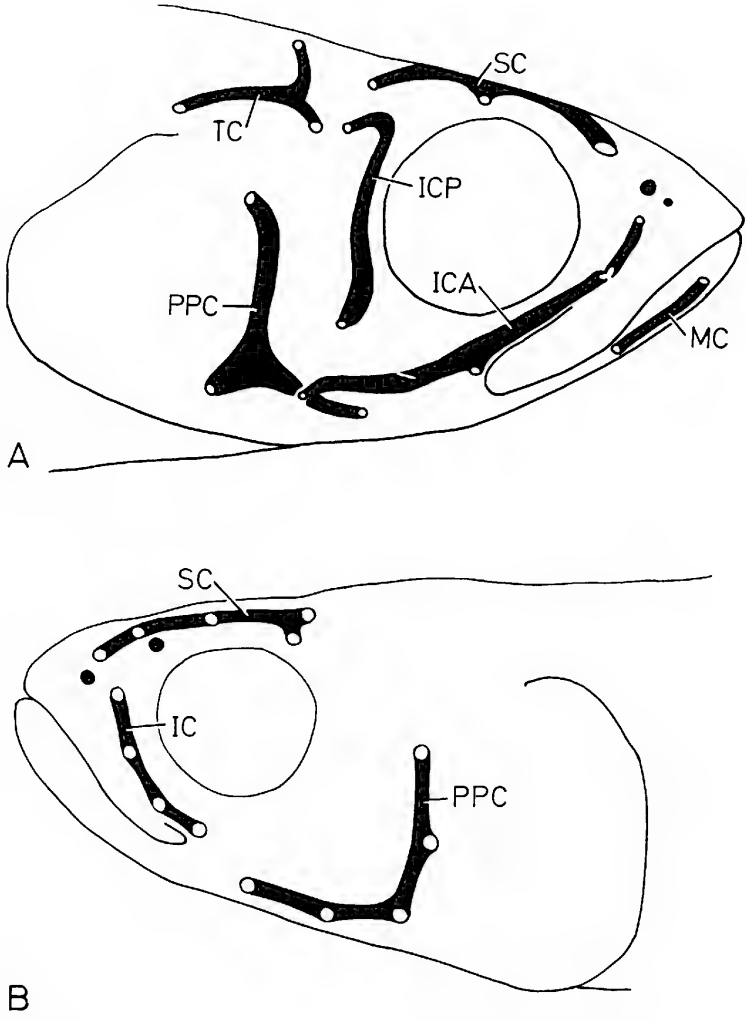


FIG. 21. Cephalic sensory canals and pores (pitlines omitted), lateral view. A. *Retropinna* sp., ANSP 106146, about 15 mm. B. *Brachygalaxias bullocki*, AMNH 3625, 9 mm.

observ.). In most species examined, mentomandibular, cheek, ethmoidal, anterior, and middle pitlines are more or less recognizable. But compared with esocoids, there are relatively few pitorgans and the pitlines are relatively indistinct. Only in *Lepidogalaxias* are pitlines well developed and distinct, resembling in general appearance those of *Dallia*. Homologs of the mandibulopreopercular, subnasal, and opercular pitlines of esocoids are apparently absent from all species.

The cephalic canal and pore patterns support the concept of the Galaxii-

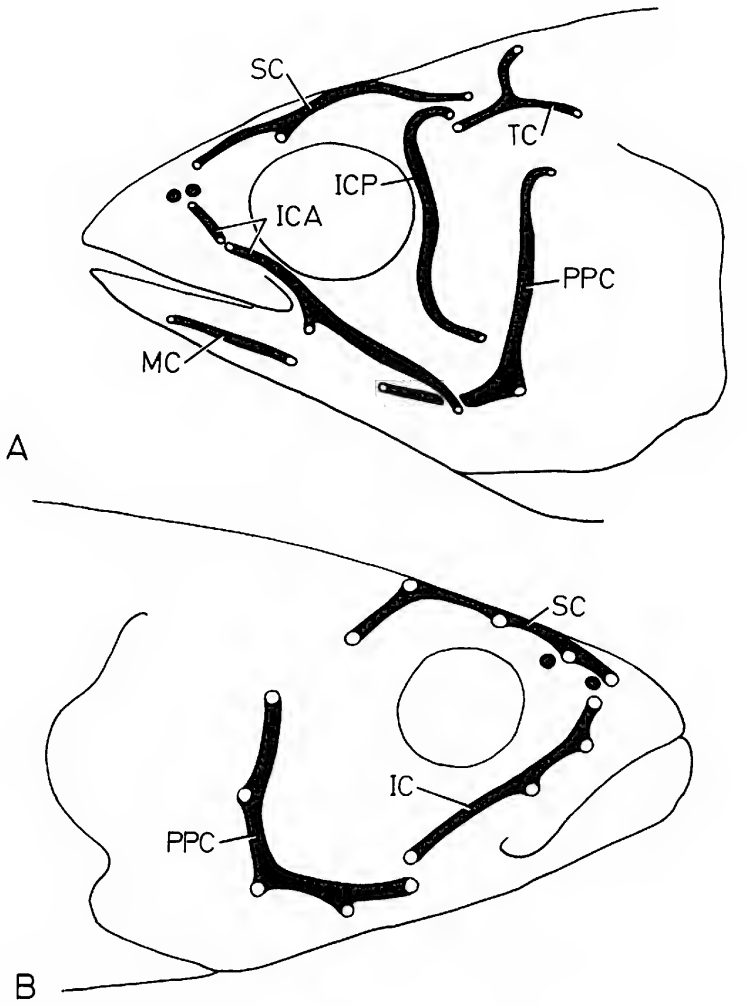


FIG. 22. Cephalic sensory canals and pores (pitlines omitted), lateral view. A. *Prototroctes maraena*, MCZ 6867, about 30 mm. B. *Aplochiton zebra*, MCZ 46272, 28 mm.

dae as a monophyletic group. Whereas the cephalic canals tend to be subdivided into separate components in other salmoniform fishes (e.g., esocoids), in none of them is the infraorbital canal modified as in galaxiids. In galaxiids, the anterior part of the infraorbital canal, enclosed in two bones (McDowall, 1969; personal observ.; bones corresponding perhaps to the lacrimal and infraorbital 2 according to Nelson, 1969c), is posteroventrally deflected, in some species extending to or beyond the anterior limit of the preopercular canal.

Certain canal and pore characters, supporting the interrelationships of galaxiids suggested by McDowall (1969), correspond to patterns (1) and (2). The low number of supraorbital (3) and preopercular (3) pores of the *Retropinna* group may be interpreted as characters advanced relative to the higher number (5 and 5–6, respectively) of the *Galaxias* group. The absence of a temporal canal and a posterior part of the infraorbital canal from the *Galaxias* group may be interpreted as characters advanced relative to the *Retropinna* group. Subdivision of the family Galaxiidae into a subfamily Retropinninae (*Prototroctes*, *Retropinna*, and *Stokellia*), and a subfamily Galaxiinae (*Aplochiton*, *Brachygalaxias*, *Galaxias*, *Lovettia*, *Neochanna*, *Nesogalaxias*, and apparently *Saxilaga* and *Paragalaxias* as well [Scott, 1935, 1936, figures what might be a *Galaxias*-type of pore arrangement for *Saxilaga* and *Paragalaxias* but only three pores are shown for the supraorbital canal of *Saxilaga*]) is suggested. The relationships of *Lepidogalaxias* remain obscure. In certain ways it resembles galaxiines (Frankenberg, MS). Galaxiines (particularly *Brachygalaxias*), in lacking temporal, posterior infraorbital and, sometimes, mandibular canals, tend to approach the highly advanced condition of *Lepidogalaxias*. *Lepidogalaxias* may be the sister group of all other galaxiines (Frankenberg, MS), but sensory canal and pore data are inconclusive. Further comparative study is called for.

Chapman (1944) noted certain peculiarities shared by galaxiid and esocoid fishes, concluded that the two groups are closely related, and suggested that they be classified together. Gosline (1960) argued that galaxiids are more closely related to osmerids, salangids, and salmonids than to esocoids (see also Nelson, 1970a; Greenwood and Rosen, 1971). There may be some advanced characters of the cephalic sensory system shared between galaxiids and esocoids, particularly between galaxiines and umbrines, in which the canal system is the most reduced, but precise comparisons have yet to be achieved and may not ever be forthcoming. Other characters of a precise sort indicate a close relationship between galaxiines and retropinnines, and a close relationship between umbrids and esocids. Compared with galaxiines and umbrids, retropinnines and esocids have the canal system more completely represented, and, in that sense, in a more primitive condition. If so, the cephalic sensory system has been similarly modified (by loss of canals and elaboration of pitlines) during the evolution of the Galaxiidae, on the one hand, and the Esocoidei, on the other. With respect to this system, more detailed studies are required to determine the degree of parallel development of homologous characters, if in fact any are present. It is apparent from other groups of teleostean fishes, e.g., the Ostariophysi (Lekander, 1949), Centrarchidae (Branson and Moore, 1962), Stichaeidae (Makushok, 1961), that tend-

encies toward canal reduction are common, and patterns similar to those of, for instance, galaxiids can be found in groups, such as the Atherinidae (fig. 23; for the Cyprinodontidae and Poeciliidae see Gosline, 1949; Rosen

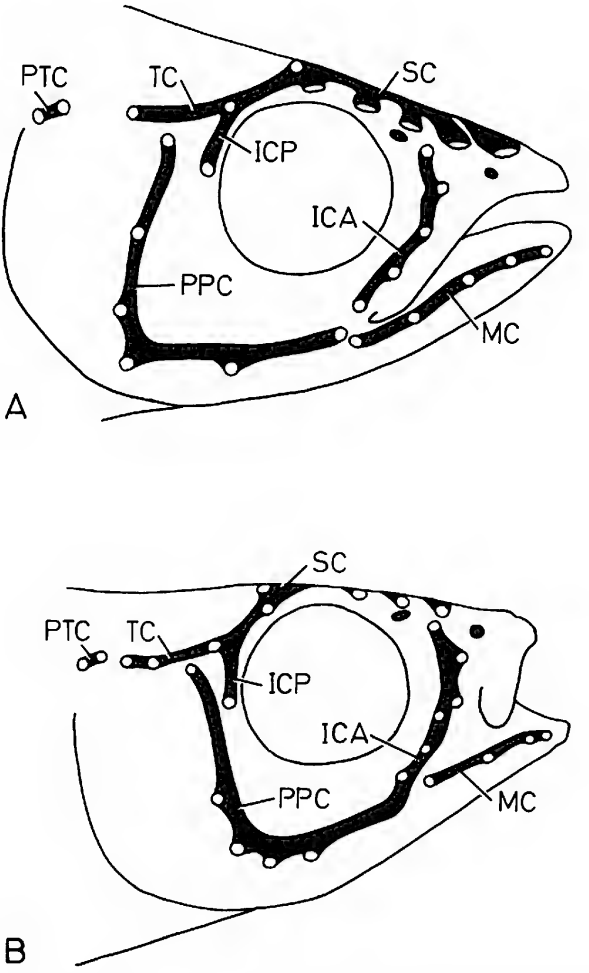


FIG. 23. Cephalic sensory canals and pores (pitlines omitted), lateral view. A. *Melanotaenia vanheurni*, AMNH 15033, 18 mm. B. *Quirichthys stramineus*, AMNH 20571, 8 mm.

and Mendelson, 1960) only remotely related to them. Without precise comparisons, general similarities such as those between galaxiids and esocoids have vague significance for determination of the degree of phyletic relationship. Thus, Chapman's proposed relationship between galaxiids and esocoids is left unsupported by the results of this study.

## CEPHALIC SENSORY CANALS IN SOME MAJOR GROUPS OF TELEOSTEAN FISHES

According to Greenwood et al. (1966, 1967) the major groups of teleostean fishes include the Taeniopedia (Division I, including Elopomorpha and Clupeomorpha), Archaeophylaces (Division II, including Osteoglossomorpha), and Euteleostei (Division III, including all other teleosts). Subsequent work has centered on the Euteleostei and its major subdivisions; the Protacanthopterygii, Ostariophysi, and Neoteleostei. The Protacanthopterygii are being gradually restricted to salmoniforms (Patterson, 1970, p. 282), and the Ostariophysi have been expanded to include gonorynchiforms (Rosen and Greenwood, 1970); all other euteleosteans have been grouped together as Neoteleostei (Rosen and Patterson, 1969; Nelson, 1969a).

The cephalic sensory system provides little evidence to evaluate the interrelationships of the major teleostean groups. Generalized members of all the major groups have the system in a condition near that primitive for teleosts as a whole. In some members of some groups, the supraorbital canal is independent — a condition possibly primitive for teleosts (see above). Further study is required to evaluate the significance of this variation.

In a discussion of iniomous (myctophiform) fishes, Gosline et al. (1966, p. 3) noted the general presence of a "cross-connection between the supraorbital canals just behind the orbits. No evidence of such a cross-connection has been found in isospondylous fishes." Such a connection is absent from osteoglossomorphs, and probably from all clupeomorphs and protacanthopterygians (personal observ.). Among elopomorphs, a supraorbital commissure occurs in some anguilliforms (Allis, 1903; Gosline 1951), but not notacanthiforms (Trotti, 1940), halosaurs, and albuloids (McDowell, MS; personal observ.); among ostariophysans a supraorbital commissure occurs in siluroids (Pollard, 1892; Collinge, 1895; Herrick, 1901; Lekander, 1949, p. 59), but not generally in characoids nor cyprinoids. Further study is required to evaluate the significance of this variation.

Members of the group Clupeomorpha have the cephalic sensory system in an advanced condition, with the formation of a recessus lateralis. This involves an approximation of the infraorbital and preopercular canals. As a result, highly ramified tubes from the infraorbital canal extend across the preopercular canal onto the opercular bones, there opening by pores to the surface (Wohlfarht, 1937; Bamford, 1941; Gunther and Demoran, 1961; Monod, 1961). A condition approaching that of clupeomorphs

occurs in *Elops* (fig. 13A), especially in *Megalops* (fig. 14A), alone among elopomorphs, and so far as known other fishes both fossil and Recent. A highly ramified canal system does occur in other fishes, for example, the Recent holosteans *Amia* and *Lepisosteus* (Allis, 1904) and Recent teleosts such as *Synodus* (fig. 14B), but either the type of ramification or the overall pattern is different. In the holosteans the ramifying networks are irregular and enclosed in dermal bones. In *Synodus* the distance between the infraorbital and preopercular canals seems secondarily increased and there is no tendency for the tubes of the infraorbital canal to extend over or behind the preopercular canal. In *Megalops*, in contrast, the infraorbital tubes extend to, but not beyond, the preopercular canal. This resemblance between *Elops*, *Megalops*, and clupeomorphs is insufficient to demonstrate that they are closely related, yet it is one advanced character indicating such a relationship. Accordingly there is some evidence to support the retention of the Clupeomorpha within the Taeniopedia (Division 1), as suggested by Greenwood et al. (1966; cf. Greenwood, 1970, p. 133).

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